Benthic community organization in the Ludlow Series of the Welsh Borderland

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Synopsis

Five areas of the Ludlow Series in the Welsh Borderland have been studied by quantitative, stratigraphic sampling to determine community organization on an Upper Silurian shelf. Measured sections show an ordered succession of predominantly terrigenous facies, with an environmental gradient of general shallowing, increasing grain size, decreasing clay content, decreasing bioturbation, and increase in storm-deposited beds of laminated silt and shells. This sequence is interrupted by low energy, back-barrier carbonates in the Upper Bringewood Beds. Shell transport occurred commonly during deposition of proximal shelf silts, and was related to a storm-generated, suspension type of movement which did not contribute to shell breakage or abrasion. Sorting of epifaunal brachiopods into concentrated layers is the most significant, taphonomic effect of transport.

Stratigraphic profiles of fauna, based on continuous series of samples at 1 m vertical intervals, are used to define six communities in measured sections, dominated by articulate brachiopods, bryozoa, molluscs and trilobites. Substrate sedimentation processes and hydrographical history of the depositional area were important factors influencing Ludlow shelf faunas, and an overall control by the physical environment appears to have shaped community organization. Decline in species diversity, increase in opportunistic species and changes in faunal composition occur along the distal to proximal shelf gradient in

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stratigraphic sections. These changes correlate with increased rates of sedimentation and frequency of storm-sedimentation events. Trophic structures in Ludlow shelf communities appear to have been relatively simple, dominated by low level suspension feeding and deposit feeding at the same sites. Encrustation of shells and rare predatory borings are the only preserved evidence of biotic interaction.

During intervals of environmental constancy, stratigraphic variation occurs within communities, but results in no biologically controlled or directional trends. In proximal shelf environments, intracommunity variation is extreme and unpredictable, but in distal shelf environments, predictable cycles in abundance of particular species occur in vertical intervals of several metres. Intracommunity variation in distal shelf environments does not conform to models of ecological succession, is not accompanied by any sedimentary changes, and is not affected by benthic faunal destructions represented by bentonites. A model of pelagic environmental effects upon larval recruitment is the best explanation for the phenomenon.

Number and discreteness of Ludlow shelf communities, as well as diversity, population strategies and faunal composition were primarily controlled by the physical environment, and the major faunal patterns in stratigraphic sections are products of the environmental history of the depositional area. Variation within particular communities and within particular habitats is superimposed upon these patterns, and is probably related mainly to pelagic effects upon larvae, with a large random component. A consequence of this simple, physically-controlled community structure is quantitative stability of composition and diversity in terrigenous shelf communities from at least early Silurian until early Devonian times. There is no evidence for 'biological accommodation', or progressive niche-partitioning, in Silurian communities of stable, distal shelf environments.

Introduction

This study is a quantitative, stratigraphic analysis of community organization in marine bottom faunas in the Ludlow Series of the Welsh Borderland. The Ludlow of this area is a sequence of dominately terrigenous strata deposited under open marine, shelf conditions. It is the uppermost division of Murchison's original Silurian System, and has been intensively studied by palaeontologists and stratigraphers for the past 140 years. Lawson (1975) has reviewed earlier work, and given an important preliminary account of ecological divisions in the Ludlow fauna.

In contrast to previous studies of Silurian palaeoecology in the Welsh Borderland, such as Hancock, Hurst & Fürsich (1974), the environmental analysis in this report is established independently of faunal data. Sedimentological study of selected measured sections has been used to establish physical, environmental gradients. The vertical sequence of Ludlow terrigenous sediments is considered as a cross-section from distal to proximal shelf depositional environments (Walther 1894 : 979). Physical sedimentary effects were far more important in determining community patterns in Silurian shelf faunas than previous studies would indicate.

Stratigraphic patterns of fauna in Ludlow sections have been described with closely spaced quantitative samples. Detailed faunal data have been derived from this sampling, and these data are related to the sedimentary-environmental gradients observed in sections. The work is not intended to provide complete areal coverage of the Welsh Borderland, or define any standard bathymetric sequence of Ludlow communities; instead, its primary purpose is a consideration of biological and environmental aspects of community organization in selected measured sections of shelf sediments.

Stratigraphic patterns in fauna within measured sections show both between and within habitat components, involving directional trends along environmental gradients and non-directional fluctuations. As a matter of convenience, these patterns are described as six named 'Associations' of species. In the concluding parts of this report, the faunal and environmental data are compared with models of ecological organization, which consider aspects of biotic interaction, environmental response and ecological succession in marine communities. This comparison establishes some of the important biological and environmental aspects of Ludlow community organization in the Welsh Borderland, and has general applicability to Silurian shelf faunas.

Methods

Stratigraphic sections

Fig. 1 shows the five areas in the Welsh Borderland where stratigraphic sections were measured.

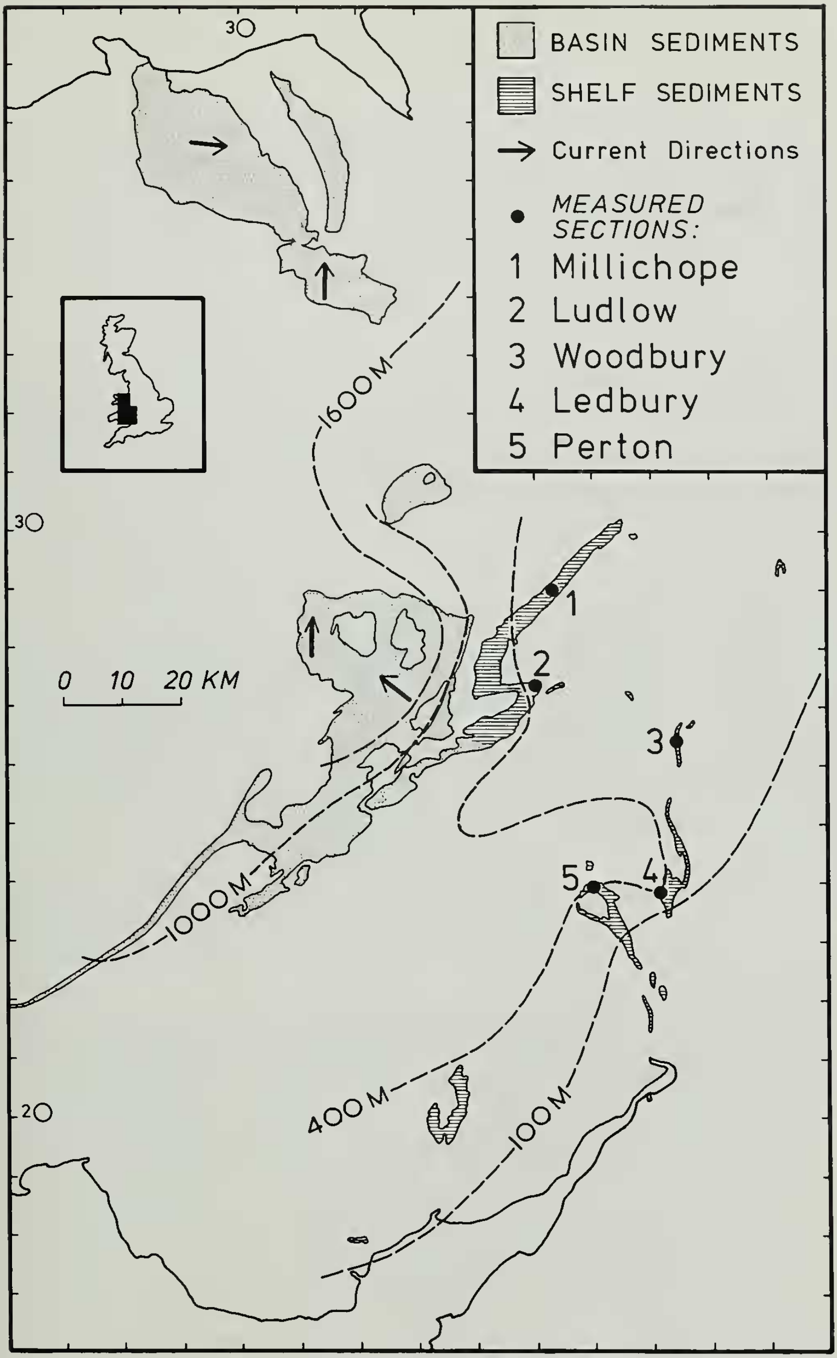

Fig. 1 Ludlow outcrop of Wales and the Welsh Borderland, showing the location of study areas. Isopachytes and current directions are adapted from Holland & Lawson (1963).

These areas were selected to obtain detailed coverage of a particular part of the Ludlow shelf deposits, and do not record the full complexity of Ludlow faunas and sediments in the Welsh Basin. Because of limited outcrop in most areas, many small, isolated sections had to be measured to obtain a composite record of the succession. The 27 separate sections are shown in Fig. 2, and their locations are described in Appendix 1, p. 258).

Sections were measured directly with tape, and the sequence and thickness of all sedimentation units recorded to the nearest cm. The principal sedimentation units recorded were bioturbated sediment, simple laminated beds, amalgamated laminated beds, bentonites and shell beds or layers. Textures were qualitatively noted in the field, and checked in the laboratory with thin sections of representative samples. Over 100 saw-cut slabs were prepared for observation of sedimentary structures.

Sampling of fauna

The purpose of palaeontological sampling was to produce a quantitative faunal profile of each stratigraphic section, based on numerous equally-spaced sampling points. Bulk rock was collected, and not individual fossils. In each section, the samples of bulk rock were taken at distances as near as possible to 1 m apart stratigraphically. Closer sample spacing was used in a few sections to study small-scale ecological phenomena, and wider spacing was necessary where rock could not be removed from sheer faces of large quarries. The 1 m spacing distance governed the location of samples, and not the presence of abundant or well-preserved fossils. This practice was modified, however, in the lowest Lower Leintwardine Beds of Woodbury and Perton Quarries, where fossils are very rare except in transported shell layers.

The stratigraphic thicknesses of bulk rock samples are given in Appendix 3, p. 268. These ranged generally from 1 to 20 cm, and most samples were about 4000 cm^3 in volume. No attempt was made to standardize sample volumes, however, and density was not the basis for palaeontological quantification. Most samples were taken from a single sedimentation unit.

The samples of bulk rock were split along fissile surfaces parallel to bedding, and all observed macrofossils were counted. One hundred and twenty-two samples were prepared in the field with hammer and chisel. These samples were restricted to low-diversity faunas of the Whitcliffe Beds, Leintwardine Beds and Upper Bringewood Beds, and were made only after eight months of laboratory work on similar samples, in which a thorough familiarity with species was obtained. The remaining 295 samples were processed in the laboratory with a mechanical rock splitter. Most fossils were decalcified with dilute hydrochloric acid to obtain internal and external moulds.

Palaeontological quantification

Because of the variation in sedimentary facies and probable rates of deposition in Ludlow shelf deposits, volumetric densities of fossils are not reliable for sample comparisons. In this study the basis for standardizing and comparing the faunal content between samples is relative abundance. Relative abundances were calculated within each sample for each taxonomic category under consideration (usually species). The relative abundance of a taxon is defined as the number of individuals of the taxon divided by the total number of individuals within the sample, expressed as a percentage. These percentages are plotted along stratigraphic columns in the sections on community definition, pp. 213–221, and form the primary basis for community analysis.

Arbitrary criteria were defined for recording over 33 000 'individuals' from the measured sections. The purpose of these criteria was consistency in quantification of samples, and not an absolute determination of the biological equivalence of different groups. Individuals were counted directly for gastropods, tentaculitids, cornulitids, annelids, hyolithids and solitary corals. Individuals were arbitrarily defined for other groups, as follows.

Brachiopods: number of individuals of a species = articulated shells + maximum number of either pedicle or brachial valves + half the number of indeterminate single valves.

Bivalves: individuals counted as for brachiopods, except that maximum number of either right or left valves was used.

Cephalopods: These fossils are preserved as phragmocones, body chambers, fragments of either, or isolated cameral and septal moulds. All pieces were scored as 1 individual, and as 2 or fewer specimens were encountered in most samples, this did not greatly exaggerate their abundance.

Trilobites: The individuals per species in each sample were counted as the number of pygidia present, or if no pygidia but other elements were present, as 1 individual. Trilobites are sufficiently rare for this method not to exaggerate their abundance in most samples.

Bryozoa: Number of individuals were defined as the number of separate bryozoan pieces observed macroscopically in each sample. No attempt was made to distinguish separate species within this phylum. Globular and encrusting bryozoa are usually preserved intact, so that 'individuals' are direct counts of colonies. Ramose forms are usually fragmented, and the number of individuals counted is partly an effect of the degree of fragmentation.

Tabulates: Number of individuals was counted as number of colonies within a sample.

Variable numbers of individuals were obtained in each sample, as indicated in Appendix 3. A detailed evaluation of the reliability of sampling, based on the number of individuals per sample, is given in Appendix 2, p. 260.

Diversity was measured within each faunal sample as the number of species obtained at a sample size of 50 individuals. This measurement was made by direct count of species in samples containing 50 individuals, and by application of the rarefaction method of Sanders (1968) to samples of larger size.

Deposition of data and collections

Only a limited amount of quantitative faunal data is presented here; full data have been deposited in the Palaeontology Library of the British Museum (Natural History), Cromwell Road, London SW7 5BD, as discussed in Appendix 3. The collections of brachiopods, cephalopods and encrinurid trilobites, representing about 85 % of total collections, have also been deposited in the Department of Palaeontology, British Museum (Natural History); specimens of other groups are deposited in the University of California Museum of Paleontology, Berkeley, Calif., U.S.A.

Stratigraphy

Stratigraphic classification of the measured sections

The stratigraphic units represented by measured sections are shown in Fig. 2, using the classification of Holland, Lawson & Walmsley (1963). Working in the type area around the town of Ludlow, these authors defined nine stratigraphic divisions. termed 'Beds,' within the Ludlow Series. They stated (1963 : 114) that 'the divisions have been mapped mainly on the basis of their faunal assemblages but lithological characteristics have also proved very helpful in their identification.' In the present study, faunal criteria have been used to recognize the divisions outside of their type sections, and the pertinent data are contained in stratigraphic profiles of fauna presented in the community definition section, p. 208, as well as Appendix 3. These criteria followed the descriptive characteristics of the divisions given by Holland *et al.* (1963), with the exceptions noted below.

The basal division of the Ludlow Series, the Lower Elton Beds, is not considered in this study. A recent account of its stratigraphical palaeoecology has been given by Hurst (1975*a*).

Recognition of the Lower and Upper Bringewood Beds

The stratigraphical position of the Bringewood Beds in the Ludlow succession is shown in Fig. 2. Although most authors have recognized a division into Lower and Upper Bringewood Beds throughout the Welsh Borderland, there has been little consistency of usage east of the type area at Ludlow. This section will define the way these stratigraphic divisions are recognized here.

Within the type area near Ludlow, Holland *et al.* (1963) defined the Upper Bringewood Beds as a silty limestone gradationally overlying calcareous siltstone of the Lower Bringewood Beds.

These authors gave full faunal lists for each division; the fauna of the Lower Bringewood Beds corresponds to the *Mesopholidostrophia laevigata* Association of this report. The Upper Bringewood Beds in the type area also contain the *M. laevigata* Association, and are faunally distinguished from the Lower Bringewood Beds by the presence of *Kirkidium knightii* and large tabulate corals (Holland *et al.* 1963). This same faunal distinction applies to the Leintwardine and Aymestrey areas west of Ludlow, the main difference being that *Kirkidium* and corals locally constitute most of the fauna of the Upper Bringewood Beds (Whitaker 1962; Lawson 1973*a*).

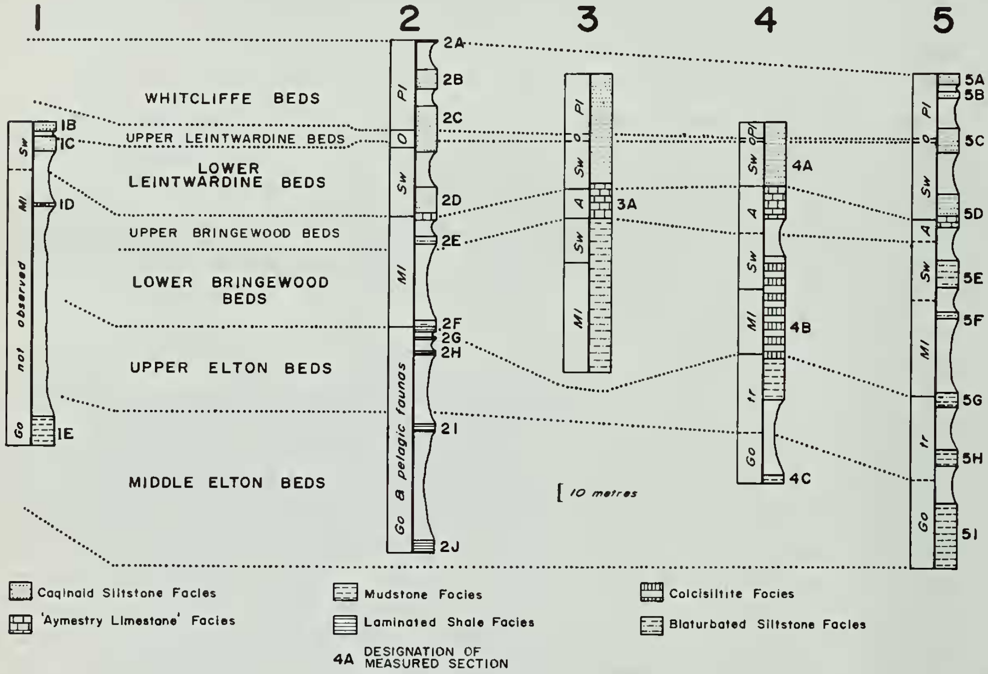

Fig. 2 Stratigraphic summary of the measured sections. Numbers refer to map locations in Fig. 1; detailed locality descriptions of each section are given in Appendix 1, p. 258. A complete sequence of all Ludlow stratigraphic units is present in every area, but only those intervals which were observed are shown. The left portion of each column indicates benthic communities as follows: *Pl – Protochonetes ludloviensis* Association; *O – Shaleria ornatella* Assoc.; *Sw – Sphaerirhynchia wilsoni* Assoc.; *A – Atrypa reticularis* – coral Assoc.; *Ml – Mesopholidostrophia laevigata* Assoc.; *tr* – transitional fauna; *Go – Glassia obovata* Assoc.

These relations are compared in Table 1 to the succession of Bringewood faunas east of Ludlow. At Woodbury Quarry and in the Perton area (Fig. 1), the *M. laevigata* Association is overlain by the lower phase of the *Sphaerirhynchia wilsoni* Association, which is in turn succeeded by the *Atrypa reticularis* – coral Association. The two lower faunas occur in calcareous siltstone, and the upper fauna in silty limestone, although both lithologies are highly gradational. Graphic charts of the species ranges which define these associations are given in Figs 17 (pp. 214–5) and 20 (p. 218), and full faunal lists are given in Appendix 3. For the purpose of this report, the Lower Bringewood Beds in these areas are defined as the *M. laevigata* Association and lower phase of the *S. wilsoni* Association, and the Upper Bringewood Beds are defined as the *Atrypa reticularis* – coral Association.

This usage differs from that of previous workers in the Woodbury and Perton areas. In the Perton Lane section, Squirrell & Tucker (1960) drew a boundary between their Lower Sleaves Oak Beds and Upper Sleaves Oak Beds at an interval which falls in the middle of section 5E of the present report (Fig. 2). This boundary was later redefined, with the Sleaves Oak Beds as the boundary between the Lower Bringewood Beds and Upper Bringewood Beds (Curtis *et al.* 1967). It falls within the lower phase of the *Sphaerirhynchia wilsoni* Association and does not correspond to the boundary of Lower and Upper Bringewood Beds recognized here.

Table 1 The definition of Lower and Upper Bringewood Beds followed in this report. The distinction of these units in the Woodbury Quarry, Ledbury and Perton areas differs from that of previous authors. In section 4B near Ledbury, Penn *et al.* (1971) placed the boundary of Leintwardine and Bringewood Beds between faunas here called the lower phase of the *S. wilsoni* Association and the *M. laevigata* Association. At Perton, Curtis *et al.* (1967) placed the boundary of Lower and Upper Bringewood Beds within the lower phase of the *S. wilsoni* Association in section 5E

	Leintwardine and Aymestrey areas	Ludlow area (type sections)	Woodbury Quarry, Ledbury and Perton areas
Lower Leintwardine Beds	upper phase of *Sphaerirhynchia wilsoni* Association	upper phase of *Sphaerirhynchia wilsoni* Association	upper phase of *Sphaerirhynchia wilsoni* Association
Upper Bringewood Beds	locally abundant *Kirkidium knightii* and tabulate corals	*Mesopholidostophia laevigata* Association with few *Kirkidium knightii* and tabulates	*Atrypa reticularis* – coral Association
Lower Bringewood Beds	*Mesopholidostrophia laevigata* Association	*Mesopholidostrophia laevigata* Association	lower phase of *Sphaerirhynchia wilsoni* Association *Mesopholidostrophia laevigata* Association

Two areas of Bringewood Beds were studied near Ledbury, section 4A, at the north end of Frith Wood, and section 4B, near Knapp Lane (see detailed locations in Appendix 1). The intervening area is poorly exposed and structurally complex (Phipps & Reeve 1969), and superpositional relations of the sections have been established on faunal grounds (Fig. 2). In section 4A, the Bringewood Beds consist of silty, nodular limestone containing the *A. reticularis* – coral Association. These strata are assigned to the Upper Bringewood Beds, and are overlain by the Lower Leintwardine Beds.

In section 4B, the Bringewood Beds consist of silty and argillaceous limestones bearing the *M. laevigata* Association in their lower portion, and the lower phase of the *S. wilsoni* Association at their top. Both faunas are assigned to the Lower Bringewood Beds, and a detailed profile of the section is shown in Fig. 19, p. 217. However, Penn *et al.* (1971 : 19) assigned strata at the top of this section, bearing the *S. wilsoni* Association, to the 'basal Leintwardine Beds'. Although ecologically similar to the fauna of the Lower Leintwardine Beds, the fauna at the top of section 4B includes *Dalejina hybrida*, *Strophonella euglypha*, *Mesopholidostrophia laevigata*, *Gypidula lata*, *Eospirifer radiatus* and *Dalmanites myops*, which are more characteristic of the Bringewood Beds.

Synchrony of Ludlow stratigraphic divisions

Holland *et al.* (1963) and most subsequent authors have considered their nine stratigraphic divisions as valid units of time for Ludlow shelf deposits of the Welsh Borderland. Lawson (1975) has noted that while most of the stratigraphic ranges of Ludlow benthic invertebrates are under facies control, the synchrony of the stratigraphic divisions is supported by graptolite evidence.

These conclusions are also upheld by the ecological analysis presented in this report. Following the concept of 'causal biostratigraphy' (Krassilof 1974), two community phenomena in Ludlow shelf sections can be explained ecologically only if they are considered synchronous. The first of these is the Upper Bringewood fauna, in which the restricted *Atrypa reticularis* – coral Association appears as a stratigraphic anomaly in inner shelf sections. This fauna can be accounted for as having occupied some sort of restrictive, back-barrier environment. There is only one interval in sections at the shelf edge area which includes barrier-type deposits, and this is the Upper Bringewood Beds containing 'banks' of *Kirkidium* and large corals. Synchrony of the Upper Bringewood Beds between these areas (as redefined in this report) is therefore highly likely.

The second synchronous ecologic phenomenon is the appearance of the distinctive fauna of the Upper Leintwardine Beds, which occupies only 1–5 m of strata in the Welsh Borderland, but occurs across the whole of the shelf area (Lawson & Straw 1956; Holland *et al.* 1963). This appearance involves the very short-lived colonization of proximal shelf deposits by forms from quiet-water, distal shelf communities. It can be explained ecologically only by brief, synchronous changes in shelf-wide current patterns controlling larval dispersal.

Both of these ecological phenomena and their causal explanations are discussed more fully on pp. 231–237. The stratigraphic position of the Upper Bringewood Beds and Upper Leintwardine Beds is shown in Fig. 2. The Middle Elton Beds, lower in the sequence, can be considered as synchronous across the Welsh Borderland by their content of *nilssoni* Zone and *scanicus* Zone graptolites (Holland *et al.* 1963, 1969; Shergold & Shirley 1968). From Fig. 2, it can be seen that synchrony of these three units effectively brackets the Ludlow shelf sequence, indicating a synchrony for each of the units between.

Sedimentology

Distinction of Ludlow basin and shelf

The Ludlow sediments of Wales and the Welsh Borderland form two environmental complexes, a basin facies to the west, and a shelf facies to the east (Fig. 1). Basin deposits range from 500 to

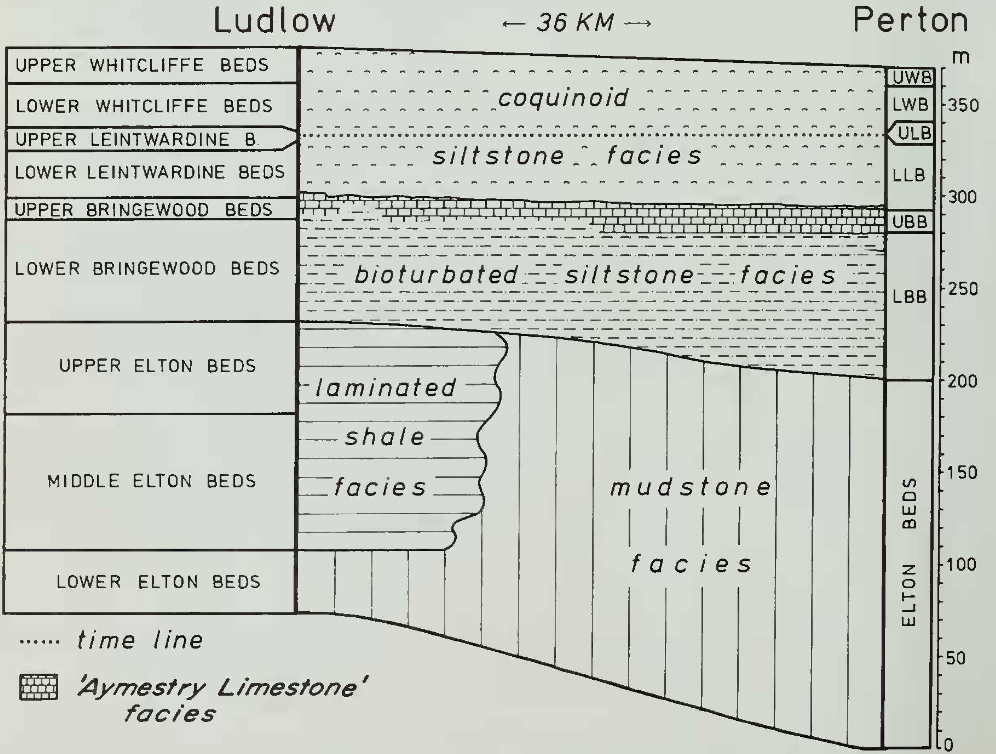

Fig. 3 Generalized cross-section showing stratigraphic relationships of the sedimentary facies described in the text.

over 1600 m thick (Holland & Lawson 1963). They consist of laminated siltstone and mudstone, siltstone and shelly turbidites, and common slumped masses of beds (Cummins 1959, 1969; Bailey 1964, 1969). The basin–shelf margin lay along the line of the Church Stretton fault, as indicated by rapid increase in sedimentary thickness to the west and westward orientation of slump directions (Holland & Lawson 1963; Bailey 1969). Cummins (1959) showed a direction of turbidite transport from the south in central Wales and from the south and west in north Wales (Fig. 1). Graptolites are most diverse throughout the Ludlow Series in Clwyd or north central Wales, indicating open-ocean connections along the north of the basin (Wood 1900; Warren 1971; Holland & Palmer 1974).

The bordering Ludlow shelf deposits are less than 500 m thick, and thin out towards the south-east (Fig. 1). They consist of bioturbated calcareous siltstone and mudstone, and include minor limestone. Depositional facies are described below for the five study areas, and are shown as a cross-section in Fig. 3. The stratigraphic sections measured within each facies are indicated in Fig. 2. This section is not an attempt to chart the complete history of Ludlow sedimentation in the Welsh Borderland, which is beset with numerous (and interesting) complexities in areas beyond the measured sections. Such a historical approach has been given by Holland & Lawson (1963), who provide a series of palaeogeographic maps. The present study is orientated toward sedimentology of vertical sections, and establishes environmental gradients used in the following palaeoecological analysis.

Petrography and diagenesis of Ludlow shelf sediments

Terrigenous sediments encountered range from equal mixtures of clay and silt to fine sandy siltstone, with quartz and mica as the predominant grains. Feldspar and other minerals comprise

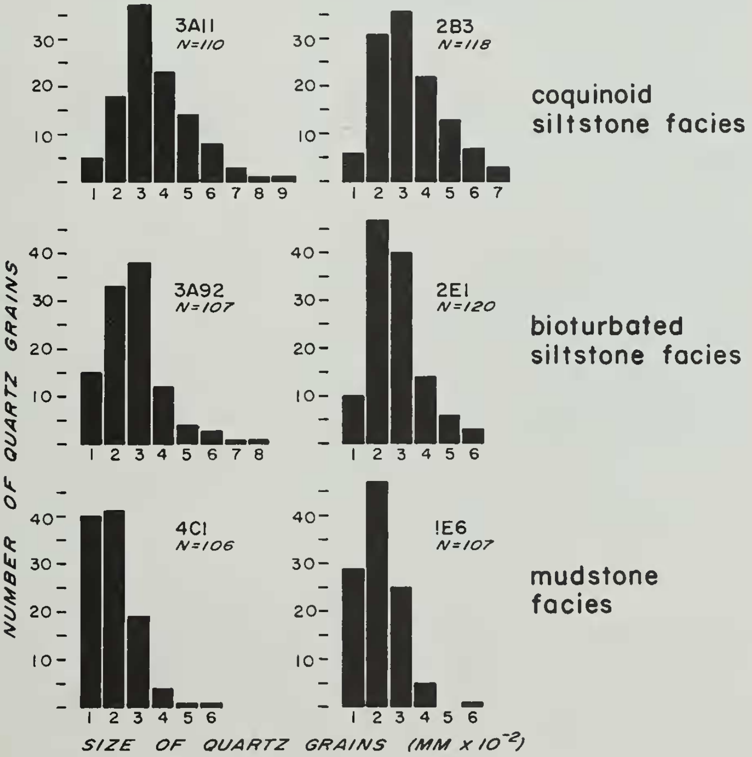

Fig. 4 Size distribution of detrital quartz grains, based on direct measurement to 0·01 mm of apparent grain diameters in thin section.

less than 2% of detrital grains. Quartz grains show low sphericity and moderate to high angularity; grain size measurements are given in Fig. 4. Clay content varies between sedimentary facies, as does the mean size of silt and sand grains. Carbonate content ranges from 7% in the finest-grained terrigenous sediments to nearly 30% in the coarsest siltstones (Holland *et al.* 1963 : 187), with marked small-scale vertical and lateral variation. Several factors suggest that much of the variation in carbonate is diagenetic – finely crystalline calcite often shows growth into detrital quartz, nodules and shell beds, discussed below, indicate diagenetic movement of carbonate, and no consistent faunal changes occur between adjacent siltstones of highly different carbonate content.

Microsparite nodules are present in all sedimentary facies. They have discrete boundaries, ellipsoidal shapes and long axes of less than 15 cm. One thin section from the Upper Elton Beds (sample 4B29) consists of 95% microsparite, 2% quartz grains, <1% mica, <1% bioclasts and 2% other material. Nodules preserve fossils three-dimensionally, in contrast to their crushed state in siltstones. In laminated beds, laminae are compressed beneath nodules and arched over their tops. Whitaker (1962) made similar observations. These features indicate post-depositional but pre-compactional formation of nodules, and attest very early diagenetic movement of carbonate.

Beds of concentrated shell material, interpreted later as high-energy storm deposits, were described by Holland *et al.* (1963) as 'shelly limestones'. These beds are usually 2–5 cm thick, and consist mainly of bioclasts and calcite cement (Table 2). In thin section, large calcite crystals are bounded by bioclasts, and completely enclose detrital grains of quartz and mica. Quartz grains show finely etched boundaries, and are sometimes intruded by small growths of calcite. Large calcite crystals completely enclosing quartz grains have also been observed in physical and optical continuity with brachiopod shells. These observations suggest replacement of quartz by calcite, and derivation of the calcite matrix from surrounding shell material. Siltstones tend to show highest carbonate content immediately around shell beds, which further suggests derivation of the calcite matrix from shells. The 'limestone' nature of these shell beds will not be considered relevant to their depositional interpretation.

Table 2 Percentage composition of shell beds based on 250–400 point counts of 1 thin section per sample. ULB – Upper Leintwardine Beds; UWB – Upper Whitcliffe Beds; LLB – Lower Leintwardine Beds; LLB – Lower Bringewood Beds

sample number	1B2	2B3	5D	5E8
stratigraphic unit	ULB	UWB	LLB	LBB
calcite cement	65	65	80	80
bioclasts	19	12	14	13
detrital quartz	6	20	5	2
detrital mica	8	3	1	3
other	2	1	1	2

Bedding

All Ludlow shelf sediments occur as tabular layers parallel to the general stratification. In the predominant bioturbated sediments, the boundaries of most layers are irregular and laterally impersistent, do not correspond to any internal sedimentary structures, and separate sediment of identical type. In Woodbury Quarry, the thick-layered strata of freshly exposed surfaces are seen to pass laterally into apparently thin-layered beds of the more weathered exposures. This type of layering, which Holland & Lawson (1963) and many others have erroneously described as 'bedding', is thus primarily a weathering feature. Primary bedding, where layers correspond to sedimentation units, is common only in the laminated shale facies of the Elton Beds and coquinoid siltstone facies of the Leintwardine Beds and Whitcliffe Beds.

Bentonites

Thin beds of clay are present throughout the Ludlow shelf facies. They are characterized by their softness, lack of fossils and sharp, parallel-sided contacts. These beds are considered as bentonites, and their thicknesses and frequency of occurrence are given in Table 3. The purest bentonites occur in the Elton Beds and Lower Bringewood Beds, where they have sharp, flat bases and appear internally homogeneous. Upper contacts are also sharp and show no burrowing, although they are overlain by thoroughly bioturbated mudstone or siltstone. Bentonites persist laterally across available outcrops.

Table 3 Stratigraphic measurements of Ludlow bentonites. EB – Elton Beds; LBB – Lower Bringewood Beds; BL – Upper Bringewood and Lower Leintwardine Beds; LLB – Lower Leintwardine Beds; UWB – Upper Whitcliffe Beds; m – mudstone facies; l – laminated shale facies; b – bioturbated siltstone facies; s – calcisiltite facies; a – 'Aymestry Limestone' facies; c – coquinoid siltstone facies

section number	1E	5H, I	2I, J	1D	2D, F	3A	5E, F	4B	3A	5D	5D	5A
stratigraphic unit	EB	EB	EB	LBB	BB	LBB	LBB	LBB	BL	BL	LLB	UWB
sedimentary facies	m	m	l	b	b	b	b	s	a	a	c	c
number of bentonite beds (* incl. derived silty claystones)	3	4	8	1	2	18*	4*	3	10*	8*	9*	1*
mean bed thickness (cm)	4·3	2·8	3·4	1·0	8·5	5·3	4·5	8·3	6·6	2·6	1·8	5·0
thickness of section (m) ÷ number of bentonite beds	5·3	11·5	1·3	3·9	3·7	4·5	4·6	16·7	2·0	0·8	1·3	6·1
bentonite beds as percent of stratigraphic thickness	0·8	0·2	2·5	0·3	2·3	1·2	1·0	0·5	3·3	3·3	1·3	0·8

In the Upper Bringewood Beds and Lower Leintwardine Beds, similar bentonites grade upward into silty claystone with well-developed parting planes. The silty claystones contain no fossils or bioturbation and may grade slightly into overlying sediment. They are often present without underlying, pure bentonites.

Mudstone facies

The mudstone facies forms most parts of the Elton Beds, and reaches thicknesses of 200 m. Sections show an extreme uniformity of texture and composition, and sedimentary structures are very rare. Clay content is about 50%, but cannot be accurately measured because of diagenesis in small mica grains. Quartz grains have an average size of about 0·02 mm, and rarely exceed 0·07 mm (Fig. 4). Shell content is generally 1–2%.

In polished section, sediments show an intricate mottling of clay-rich, dark-coloured areas and more silty, light-coloured areas (Pl. 1, fig. 5). Mottled sediment shows no discrete burrows, except for possible vertical burrow fillings of shell debris. In a few samples, mottling can be traced through intermediate stages into well-defined laminae with burrow disruptions (Pl. 1, fig. 4). Thus, the typical, mottled character of the facies results from intense deformative bioturbation.

Laminated silt beds comprise less than 1% of stratigraphic sections. They occur as isolated tabular layers 3 cm or less thick, and are continuous across outcrops of 1–2 m in extent. These beds have sharp, nearly flat erosional bases and bioturbated tops (Pl. 1, fig. 6). Parallel laminae reach thicknesses of 1 mm, and are defined by alternation of clay-rich and clay-poor silt. Maximum grain size reaches 0·2 mm, and a thin basal layer of shell debris is sometimes present. Low-angle, planar cross lamination may also occur.

A bedding type resembling the laminated shale facies occurs between 1·3 and 2 m above the base of section 5G at Perton, where beds with sharp, flat bases contain parallel lamination and grade upward into bioturbated mud and silt. They are repetitively developed at 5 cm intervals.

Laminated shale facies

The laminated shale facies reaches thicknesses of 200 m, and forms the Middle and Upper Elton Beds of the Ludlow area. Most of this sediment is identical in composition and texture to the mudstone facies, and is also very uniform in vertical profile. Bioturbation is restricted or absent through most of the facies, and the sediments have a flat, parallel lamination or well-developed parting which suggests lamination. Laminations reach 2 mm thick, and are defined by variations in clay content.

Additional sediment types occur in the Upper Elton Beds. Beds of highly calcareous, argillaceous siltstone range from 2 to 5 cm thick, with sharp, parallel, laterally continuous contacts. Graded siltstone beds also occur, reaching 2 cm in thickness with flat erosional bases. Williams & Prentice (1957) described slump structures in the Upper Elton Beds ranging from a few mm to 2 m in scale.

Bioturbated siltstone facies

The bioturbated siltstone facies is characteristic of the Lower Bringewood Beds, and forms the Upper Bringewood Beds in the Millichope area and places around Ludlow. It reaches 80 m in thickness. Except for sporadic shell beds, vertical profiles show little variation in composition and texture. Clay is present throughout, but is less abundant than silt. Quartz shows a modal grain size of 0·02–0·03 mm (Fig. 4), and may reach sizes of 0·16 mm. Shell material comprises about 1·5% of sediment volume outside of shell beds.

Most sediment shows complex mottling like that of the mudstone facies (Pl. 1, fig. 3). Traces of thin, burrow-disrupted lamination occur sporadically, and mottling is a result of intense bioturbation. *Chondrites* and small subvertical burrows are often present. Shell fragments occur in ill-defined lenticles 0·5–7 cm across which may be the result of burrowing.

Plate 1

Bioturbated Siltstone Facies

Fig. 1. Bioclastic bed within bioturbated silt, showing sharp lower contact and disturbed upper surface. Sample 5E8, Lower Bringewood Beds, Perton Lane. SO 596398.

Fig. 2. Parallel-laminated silt bed within finer-grained bioturbated silt, showing cross-sections of horizontal burrows. Near sample 3A54, Lower Bringewood Beds, Woodbury Quarry. SO 743637.

Fig. 3. Thin layer of bioclasts (interpreted in text as 'swell-lags') within bioturbated silt. Sample 3A57, Lower Bringewood Beds, Woodbury Quarry. SO 743637.

Mudstone Facies

Fig. 4. Interbedded laminated silt and mud showing the effects of intense bioturbation. This sample is from a transitional interval between the Mudstone Facies and Bioturbated Siltstone Facies. Sample 5G6, Upper Elton Beds near Perton. SO 592395.

Fig. 5. Typical appearance of the Mudstone Facies, showing mottling produced by intense deformative bioturbation and scattered, variably orientated shell material. Sample 4C1, Middle Elton Beds near Ledbury. SO 715386.

Fig. 6. Upper portion of a rare laminated silt bed, showing subvertical burrows extending from overlying bioturbated mudstone. Sample 5H3, Upper Elton Beds near Perton. SO 592394.

All figures are untreated rock slabs cut vertically to bedding; scales equal 1 cm.


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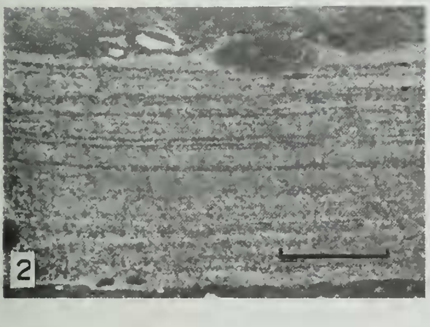
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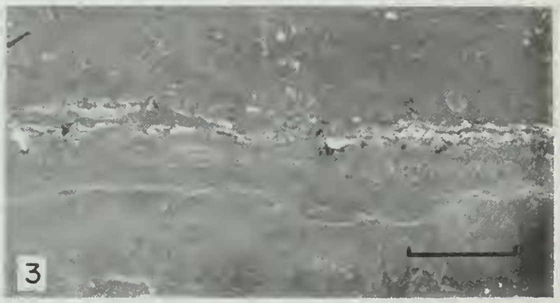
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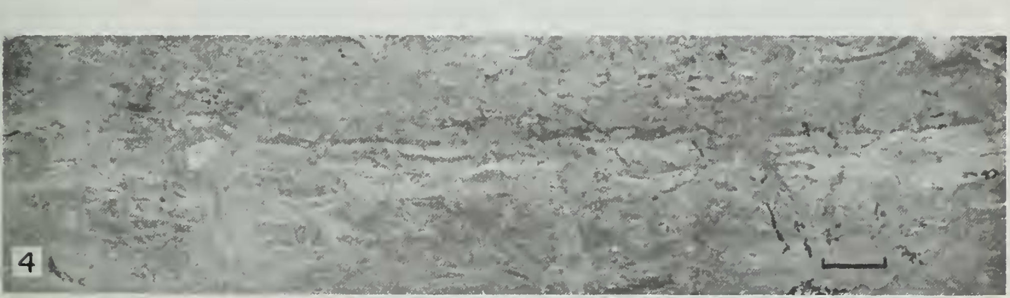
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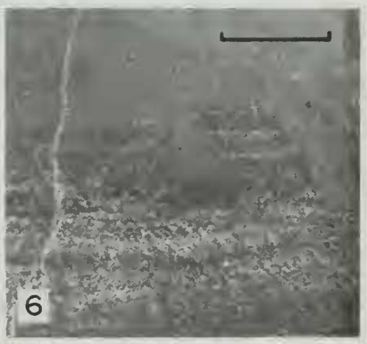
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Non-bioturbated, primary bedding composes about 4% of the facies. Isolated beds of laminated siltstone are identical to those of the mudstone facies (Pl. 1, fig. 2). Lenticular beds of shells and shell fragments also occur, and are generally 1–4 cm thick and less than 2 m in apparent length. Bases of beds are sharp erosional contacts. Upper surfaces are intensely bioturbated, with stringers of shell debris incorporated into the overlying siltstone (Pl. 1, fig. 1). Very thin layers of shell fragments and convex-upwards shells lying parallel to the bedding also occur throughout the facies, showing many burrow disruptions (Pl. 1, fig. 3). They have an average frequency of about 1 layer per 40 cm of vertical section.

Calcisiltite facies

The calcisiltite facies forms the Lower Bringewood Beds in the immediate area of Ledbury, and is a very local lateral equivalent of the bioturbated siltstone facies. It is 53 m thick, and is shown in detail in Fig. 19, p. 217. The sediment consists of very calcareous siltstone and gradational silty and argillaceous limestone. One thin section of the purest limestone is composed of 89% microsparite, 3% bioclasts, 7% mica and argillaceous material and 1% quartz grains. Most sediment, however, contains at least 50% terrigenous material.

Bioturbation is apparent throughout the calcisiltite facies by scattered, variably orientated shell material and the presence of *Chondrites*. Flat continuous weathering planes, traceable for several metres laterally, probably represent the original bedding. These planes contain local concentrations of convex-upwards shells. Thin, lenticular shell beds, identical to those of the bioturbated siltstone facies, also occur. Minor stratigraphic variations within the calcisiltite facies are shown in Fig. 19.

'Aymestry Limestone' facies

This facies comprises the Upper Bringewood Beds and basal Lower Leintwardine Beds of the Woodbury Quarry, Ledbury and Perton areas, and reaches 15 m in thickness. It is also present at the type boundary of these two units near Ludlow. One thin section from sample 5D11, from the Upper Bringewood Beds at Perton Quarry, consists of 93% microsparite, 2% quartz grains and 1% mica and argillaceous material. The limestone is generally siltier, however, and shows all gradations to highly calcareous siltstone. Microsparite nodules comprise 15% of the facies by volume.

In unweathered exposures, the only definition of bedding in this facies are thin bentonites, which divide the limestone into layers 0·5–2 m thick. This thick-bedded aspect of the facies can be seen in the Upper Bringewood Beds shown in Pl. 3, fig. 2 (p. 195). Sedimentary structures have not been observed within these layers, except for a single parallel-laminated bed observed at Woodbury Quarry. This may reflect intense bioturbation. Shells are usually rare and widely scattered, but sometimes occur in concentrated layers immediately below bentonites.

This facies extends upwards into the basal few metres of the Lower Leintwardine Beds, as determined by faunal content. These occurrence are distinguished, however, by beds of concentrated shell material and parallel-laminated, silty limestone with sharp erosional bases. Although compositionally like strata of the Upper Bringewood Beds, the limestones of the basal Lower Leintwardine Beds show periodic higher energy conditions. They grade upwards into the coquinoid siltstone facies, which contains similar sedimentary structures.

The preceding description of the 'Aymestry Limestone' facies applies only to the Woodbury Quarry, Ledbury and Perton areas, and section 2D near Ludlow. Upper Bringewood carbonates west of Ludlow, in the area between View Edge and Aymestrey, are distinguished by a dominant, sparry texture, common sedimentary structures, and common shell beds. These carbonates represent a more high-energy environment, and are located along a postulated shelf-edge barrier zone. Two depositional facies occur in this area, one characterized by common trough cross-bedding and deflation deposits of *Kirkidium*. The second facies is developed as thin tabular beds with great lateral continuity, and probably represents down-slope redeposition of carbonate sediment. A facies analysis of Upper Bringewood carbonates throughout the northern Welsh Borderland will be detailed in a separate publication.

Coquinoid siltstone facies

The coquinoid siltstone facies forms the Leintwardine Beds and Whitcliffe Beds, and reaches 80 m in thickness. Clay content is low, and silt and shell material predominate. Average grain size of quartz is 0·03–0·04 mm, and about 10% of grains are of fine sand grade (Fig. 4). Minor vertical variations in texture are common.

Bioturbation is present throughout the facies, varying from discrete burrows in laminated beds to intricate, deformative mottling (Pl. 2, figs 1, 2, 5). Primary bedding has been destroyed in about 75% of measured sections. In general, however, bioturbation is not as intense as in other terrigenous facies, and small traces of lamination commonly remain.

Shell beds comprise an average of 3% of the facies, but are highly variable in abundance between sections (Table 4). Shell material accounts for 5–20% of bed volume, and may be parallel to bedding and convex-upwards, or without consistent orientation (Pl. 2, fig. 4). Quartz grains in shell beds reach larger sizes than in the surrounding sediment, and may exceed 0·2 mm. Rounded intraformational pebbles below 5 cm in size occur in shell beds of the Lower Leintwardine Beds.

The shell beds have erosional bases which are usually flat and parallel to the general stratification. Occasionally they fill small scours less than 5 cm deep and 20 cm across. The beds are variable in thickness (Table 4), usually below 5 cm, and form small sheets, thickest centrally and thinning towards their margins; they usually extend less than 5 m laterally. Where bioturbation is minimal, shell beds form the basal layers of laminated sheets of silt (Pl. 2, fig. 4). Upper boundaries of shell beds are marked by a sharp reduction in shell density, their matrix being sometimes in textural continuity with the overlying laminated silt. As shell beds pinch out laterally, they are replaced by laminated siltstone, and a laminated siltstone sheet may have several separate lenses of shells along its base. All gradations exist between single basal shell layers and shell beds up to 10 cm thick. Bioturbation has often destroyed the laminations above shell beds, and burrowing may disrupt their upper contacts.

Table 4 Stratigraphic measurements of shell beds in the coquinoid siltstone facies. ULB – Upper Leintwardine Beds; LLB – Lower Leintwardine Beds; UWB – Upper Whitcliffe Beds; LWB – Lower Whitcliffe Beds; WB – Whitcliffe Beds, undifferentiated

section number	1B	1C	2B	2C	3A	3A	4A	5A	5C
stratigraphic unit	ULB	LLB	UWB	LWB	WB	LLB	LLB	UWB	LLB
number of shell beds	6	14	9	4	5	17	27	5	9
mean bed thickness (cm)	6·8	4·2	1·8	2·0	3·6	2·5	4·8	1·8	3·3
thickness of section (m) ÷ number of shell beds	0·65	0·46	1·16	5·74	6·00	0·97	0·49	1·22	0·64
shell beds as percentage of stratigraphic thickness	10·5	9·1	1·5	0·3	0·6	2·6	9·7	1·5	5·2

Laminated siltstone forms 22% of the facies (Pl. 2, fig. 1). Laminae are usually 0·5–1 mm thick, but may reach thicknesses of 3 mm. They consist of alternations of quartz-dominated silt and clay-rich, mica-dominated silt. Laminae consist locally of pure, uniformly-orientated biotite. Laminated siltstone forms tabular continuous sheets with nearly flat erosional bases. Where not disrupted by bioturbation, the sheets are continuous across outcrops reaching 10 m in lateral extent. Some detailed stratigraphic distributions of these beds are shown in Fig. 10 (p. 201) and Figs 16, 18 and 20 (pp. 213–218).

In the Lower Leintwardine Beds, Upper Leintwardine Beds and Lower Whitcliffe Beds, laminated siltstone usually occurs as isolated sheets within sequences of bioturbated siltstone. These sheets are less than 10 cm thick and have intensely bioturbated tops. In Perton Quarry, however, bentonites have preserved upper surfaces of sheets with symmetrical ripple marks 1–2 cm in height and 20–30 cm in apparent length. Sheets are formed internally of flat to slightly wavy parallel lamination. Small ripple bedding, as defined by Reineck & Singh (1973), is also present.

The Upper Whitcliffe Beds contain more laminated siltstone, with smaller intervals of bioturbated sediment (Figs 16 and 20). Thin, laminated sheets like those described above occur. Other laminated sheets reach 50 cm in thickness. These have nearly flat erosional bases and bioturbated tops. Internally, they consist of several distinct beds with erosional contacts, often showing a number of basal shell layers and two or three stages of minor burrowing; often beds are cut out completely at the base of other beds. They contain wavy, parallel lamination or small ripple bedding. Cross sets are generally 2 cm or less thick, of both planar and trough form, and orientated at less than 5° to the general stratification.

Another type of laminated siltstone sheet reaches 20 cm in thickness and contains parallel, even lamination throughout. In contrast to other beds, these sheets may completely lack bioturbation. Siltstone sheets containing convoluted laminae are also present. One such sheet, which defines the base of the Upper Whitcliffe Beds at Ludlow, has a lateral extent of at least 500 m (Holland *et al.* 1963).

The storm-related model of shelf sedimentation

Gadow & Reineck (1969) and Reineck & Singh (1972) described modern shelf sediments, in the Mediterranean and North Sea, which consist of bioturbated mud with interbedded sheets of laminated sand and silt. Laminated sheets have nearly flat erosional bases, infrequent basal shell layers and bioturbated upper surfaces. They decrease in thickness with increasing distance from shore. Similar beds from the Georgia shelf were described by Howard & Reineck (1972).

These authors proposed a storm-related model of shelf sedimentation. Normal shelf deposition consists of settling of suspended silt and clay which is thoroughly reworked by burrowing. During storms, sand or silt is eroded from nearshore areas and transported onto the shelf by retreating waves and ebb currents. In the southern North Sea, sand from tidal flats is carried and redeposited as far as 50 km out onto the shelf (Gadow & Reineck 1969). Minor erosion of the shelf surface, sometimes accompanied by emplacement of a shell layer, is followed by rapid settling of sand or coarse silt as tabular, laminated sheets. This may be followed by rapid settling of suspended mud. Reineck & Singh (1972) considered the sand or coarse silt to be transported in a turbidity-current fashion as 'clouds' of material which settle as the energy of transport decreases. Goldring & Bridges (1973) reviewed the general features of laminated sheets in ancient and modern shelf sediments, and also concluded that very rapid turbidity-current type deposition is involved.

Storm-related models of sedimentation have also been applied to Jurassic and Devonian shell beds by Brenner & Davies (1973) and Bowen, Rhoads & McAlester (1974). These shell beds form erosively-based sheets several cm thick within finer-grained, often bioturbated sediment. In the

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Plate 2

Coquinoid Siltstone Facies

Fig. 1. Portion of a tabular bed of cross-laminated silt, with large subvertical burrow. Section 1C, Lower Leintwardine Beds near Millichope Park. SO 529890.

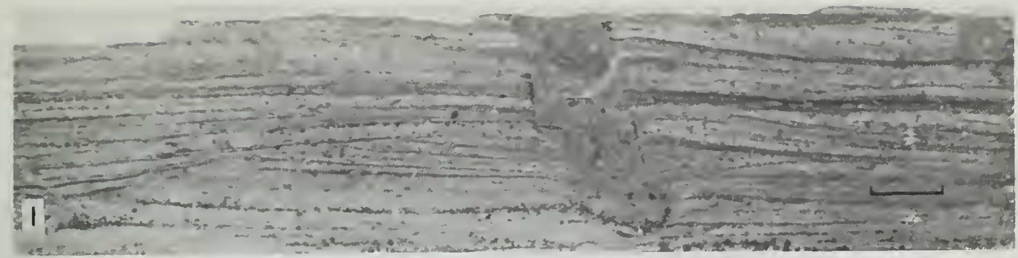
Fig. 2. Small-scale relations of laminated silt, bioturbated silt and bioclastic layers, showing incipient destruction of bedding by burrowing. Section 5A, Upper Whitcliffe Beds, Perton. SO 597403.

Fig. 3. Detail of quarry face showing dominantly tabular bedding in the uppermost portion of the Coquinoid Siltstone Facies. Most of the beds shown represent 'amalgamated sheets' of laminated siltstone. Section 5A, as last.

Fig. 4. Bioclastic layer resting on bioturbated silt and overlain by laminated silt. The shelly layer and laminated silt are attributed to rapid sedimentation during a single storm event. Sample 5A4, Upper Whitcliffe Beds, Perton. SO 597403.

Fig. 5. Burrowing in a laminated silt bed, showing vertical sections of the trace fossil *Chondrites*. Sample 4A28, Upper Leintwardine Beds, Frith Wood, near Ledbury. SO 722402.

Figures 1, 2, 4 and 5 are untreated rock slabs cut vertically to bedding; scales equal 1 cm.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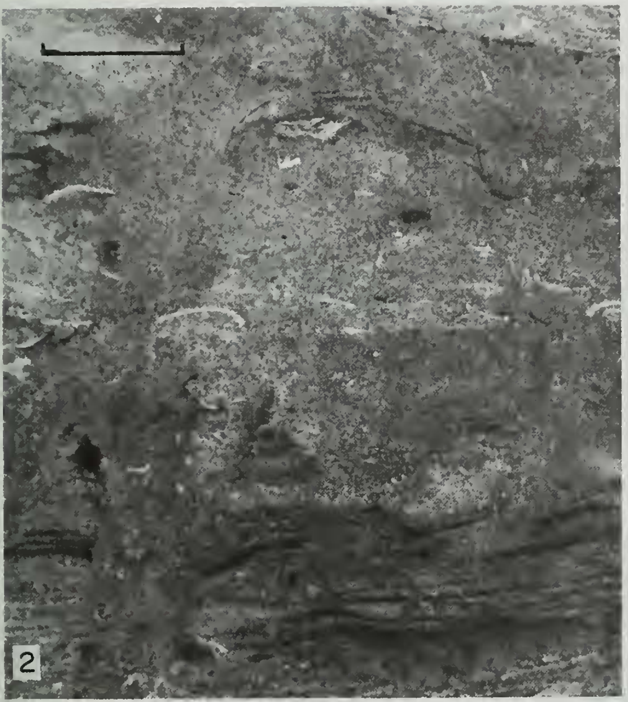
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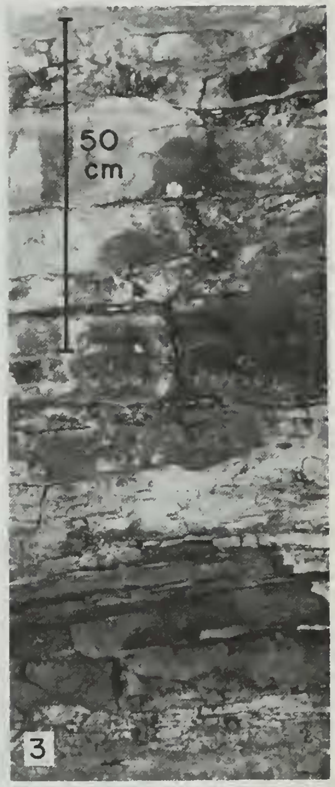
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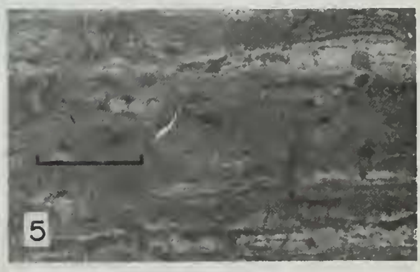
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Jurassic examples, shell beds contain larger detrital grains than the surrounding sediment, and in the Devonian example they are overlain by laminated sheets of siltstone. The shell beds represent higher depositional energies than the sediments with which they are intercalated, and Brenner & Davies (1973) and Bowen *et al.* (1974) related them to rapid transport and deposition during storms. Bridges (1975) has made similar interpretations for shell beds at the base of laminated sandstones in Llandovery shelf deposits.

Application of the model to Ludlow shelf sediments

The Ludlow terrigenous facies in the Welsh Borderland are directly comparable to modern shelf sediments in consisting of an alternation of bioturbated silt and clay with coarser-grained, laminated sheets of silt (Pl. 1, fig. 2). Laminated siltstone sheets in Ludlow facies represent rapid, turbidite-type deposition during storms. Shell beds are genetically related deposits, and represent the traction load, or initially-settling coarse fraction, during mass transport of silt. Emplacement of sheets of shells and laminated silt was accompanied by very little erosion of the Ludlow shelf. This is indicated by their flat, generally non-scoured bases, and also by faunal evidence. As discussed later, shell beds consist almost wholly of epifauna, with significantly fewer infaunal shells than in bioturbated sediment. Lingulids, for example, were very rarely scoured from their burrows on the Ludlow shelf. In the bioturbated siltstone facies, 95% of observed lingulids occur in vertical life position (N=55), and 81% are in life position in bioturbated sediment of the coquinoid siltstone facies (N=26). These relations indicate that sediment deposited in the study area remained essentially in place. Palaeocurrent directions indicate that sources of the storm-derived silt were probably from the south and east (Bailey & Reese 1973).

Terrigenous deposits of the measured sections show a stratigraphic succession from the mudstone facies, through the bioturbated siltstone facies to the coquinoid siltstone facies (Fig. 3). This succession shows the following trends:

1. Upward decrease in clay content, shown relatively in Table 5 by the increase in volumetric proportion of quartz grains.

Table 5 Quartz composition of Ludlow terrigenous facies, based on 100–250 point counts on one thin section per sample. S – sample number; Q – percentage of detrital quartz. The general increase in quartz percentage from the mudstone facies to coquinoid siltstone facies is a general reflection of a decreasing amount of clay within sediments

mudstone facies Elton Beds		bioturbated siltstone facies Bringewood Beds		coquinoid siltstone facies Leintwardine and Whitcliffe Beds	
S	Q	S	Q	S	Q
1E6	20%	1D10	34%	2B3	59%
4C1	24%	2E1	27%	2C7	55%
		3A92	27%	3A11	45%
		5E3	26%	3A14	49%
		5F1	21%	5A4	49%

2. Upward increase in average silt size, with sand appearing high in the succession (Fig. 4).
3. Upward decrease in bioturbation, from over 99% destruction of primary sedimentary structures in the mudstone facies to about 75% destruction in the coquinoid siltstone facies.
4. Upward increase in frequency and thickness of laminated sheets of siltstone and shell beds.
5. Upward trend towards reworking and sediment dilution of bentonites.

These trends indicate a general increase in sedimentation rate, energy level and proximity to sediment source. The mudstone facies represents a distal, shelf, quiet environment, as indicated by fine grain size, intense bioturbation and stratigraphic position at the initiation of a marine deepening in the Welsh Borderland (Hurst 1975*a*). Sedimentation appears to have been dominantly from suspension, and the rarity of laminated siltstone sheets indicates lack of storm influence and distance from sources of redeposited sediment. The bioturbated siltstone facies also represents a distal shelf environment removed from sediment sources, but increasing agitation is apparent by frequent concentrations of shell material. These concentrations are compared to 'swell lags' in following sections, and related to the distal passage of wave motion (but not transported sediment) during storms.

The coquinoid siltstone facies completes the Ludlow terrigenous cycle, and represents a proximal shelf environment, nearer to the sediment source, and subject to frequent storm sedimentation. The culmination of this trend is seen in the Upper Whitcliffe Beds, where convolute laminations and the predominance of laminated siltstone sheets indicate the highest sedimentation rates. The amalgamated sheets of siltstone in this interval probably represent close proximity to sources of redeposited sediment (Goldring & Bridges 1973).

Significance of the laminated shale facies

The laminated shale facies is laterally equivalent to the mudstone facies (Fig. 3), and also represents a very low-energy, distal shelf environment. Although identical in texture and composition to the mudstone facies, it differs in its lamination and rarity of bioturbation. Rhoads & Morse (1971) identified very low oxygen concentrations as a major restrictive factor for bioturbating organisms of offshore shelves. Where concentrations of bottom oxygen reach their lowest levels in the Santa Barbara Basin and Gulf of California, shelf muds preserve complete lamination, and have few burrowing organisms (Emery & Hülsemann 1962; Calvert 1964). Low oxygen level and rarity of burrowers can be considered a major environmental distinction of the Ludlow laminated shale facies.

The relation of Ludlow carbonates to the terrigenous shelf succession

The 'Aymestry Limestone' facies of the Upper Bringewood Beds and basal Lower Leintwardine Beds in sections studied here is an interruption of the terrigenous succession discussed above (Fig. 3). From Ludlow to the Ledbury area, the 'Aymestry Limestone' facies can be characterized as quiet-water and offshore, but otherwise shows no sedimentary features diagnostic of a specific environment. Its fauna, the *Atrypa reticularis* – coral Association, is a depauperate assemblage compared with the underlying bioturbated siltstone facies, which suggests some restrictive type of environment.

According to the correlation presented in Table 1, p. 181, these carbonates are equivalent in age to high-energy, *Kirkidium*-bearing limestones of the shelf edge area. Alexander (1936) and Lawson (1973*a*) considered these shelf-edge limestones as very shallow-water in nature and possibly forming a low submarine ridge. This interpretation is supported by the sedimentary observations given earlier. From these relations, we can conclude that the low-energy 'Aymestry Limestone' facies of the study area represents a back-barrier deposit, formed under deeper, quieter water than the high-energy limestones at the relief edge.

Phipps & Reeve (1967) and Lawson (1973*a*) have considered Upper Bringewood carbonates as the shallowest part of a Lower Ludlow shoaling cycle, followed by transgressive or deeper-water conditions during deposition of the Lower Leintwardine Beds. This interpretation is valid for the shelf edge regions around Leintwardine and Aymestrey, outside the present study area. Interpretation of an Upper Bringewood shallowing, followed by deepening in Lower Leintwardine times, is not valid for the areas considered in this study, however, and ignores important differences between shelf edge and inner shelf areas. These differences may be listed as follows:

Shelf edge (Leintwardine, Aymestrey areas)	Inner shelf (Woodbury Quarry, Perton areas)
Upper Bringewood Beds comprising carbonates with high-energy sedimentary structures and abundant sparite	Upper Bringewood Beds of massive, low-energy carbonate of microsparite and argillaceous material
Upper Bringewood Beds end with an erosional surface at the base of the overlying Lower Leintwardine Beds, with abrupt faunal change	Continuous sedimentary and faunal transition, with no erosional breaks between the Upper Bringewood Beds and Lower Leintwardine Beds
Basal Lower Leintwardine Beds often very clay rich, and often with relatively poor bioturbation and partially preserved, parallel lamination	Lower Leintwardine Beds typical of coquinoid siltstone facies described earlier, continuing terrigenous sedimentary trends from the Lower Bringewood Beds

The low-energy 'Aymestry Limestone' facies of the study area appears to represent a pause in the progression of terrigenous shelf deposits over the Welsh Borderland, related to reduced terrigenous supply and local elevation of a barrier zone at the shelf edge. These low-energy carbonates grade upward into the coquinoid siltstone facies of the Lower Leintwardine Beds, which continues the general progressionary trend of terrigenous facies. Lawson (1973*a*) has referred to a basal conglomerate of regional development as the beginning of Lower Leintwardine deposition. An uninterrupted sedimentary transition from the Upper Bringewood Beds to the Lower Leintwardine Beds can be observed in the type section near Ludlow and at Woodbury Quarry and Perton Quarry (Pl. 3, fig. 2). Measurement of these sections cm by cm has failed to reveal a basal Lower Leintwardine conglomerate. Several laminated siltstone sheets in the lowest several metres of the Lower Leintwardine Beds in Woodbury and Perton Quarries include scattered pebbles of limestone and calcareous siltstone. These pebbles almost certainly relate to minor intraformational erosion during storms. They do not represent a discrete basal conglomerate, and do not indicate an abrupt change in regional depositional conditions.

Shell occurrence

Disturbed neighbourhood assemblages and transported assemblages

Ludlow shell occurrences can be assigned to two general taphonomic categories defined by Scott (1974). Transported asemblages consist of shells which have been mechanically deposited during sedimentation. This term refers to a process, and has no implicit connotations of distance or ecological mixing. In Ludlow sediments, these assemblages consist of storm-related shell beds as described earlier, associated with erosional surfaces and laminated sheets of siltstone. Examples are shown in Pl. 1, fig. 1 and Pl. 2, fig. 4. Other transported assemblages are formed of convex-upwards shells which are closely packed in layers parallel to bedding (Plate 4, p. 225).

Scott (1974) defined a disturbed neighbourhood assemblage as fossils which have been shifted from their life positions, but not significantly moved or mixed ecologically. Bioturbation is the common agent of disturbance. These assemblages have been identified in this study by a dispersed, inconsistently orientated scatter of shells within bioturbated sediment (Pl. 1, fig. 5). This is the most common type of shell occurrence in Ludlow shelf sediments.

Plate 3

Fig. 1. Vertical saw-cut section of the Ludlow Bone Bed from the type locality at Ludford Lane, Ludlow. In this sample the bone bed is developed as two layers of bone material, the lower one being barely visible in the lower left of the figure. Note the sharp contacts of the upper layer of bone material, and the overlying parallel-laminated silt; compare with Pl. 2, fig. 4. These features are indicative of storm-related redeposition of sediment rather than in-place accumulation of the bone material, as discussed in text. Scale in figure indicates 1 cm.

Fig. 2. Perton Quarry (designated as section 5D in this report), showing the Upper Bringewood Beds ('Aymestry Limestone' Facies) and Lower Leintwardine Beds (Coquinoid Siltstone Facies). Note the laterally continuous. tabular character of bedding. Photograph by Charles Aithie.


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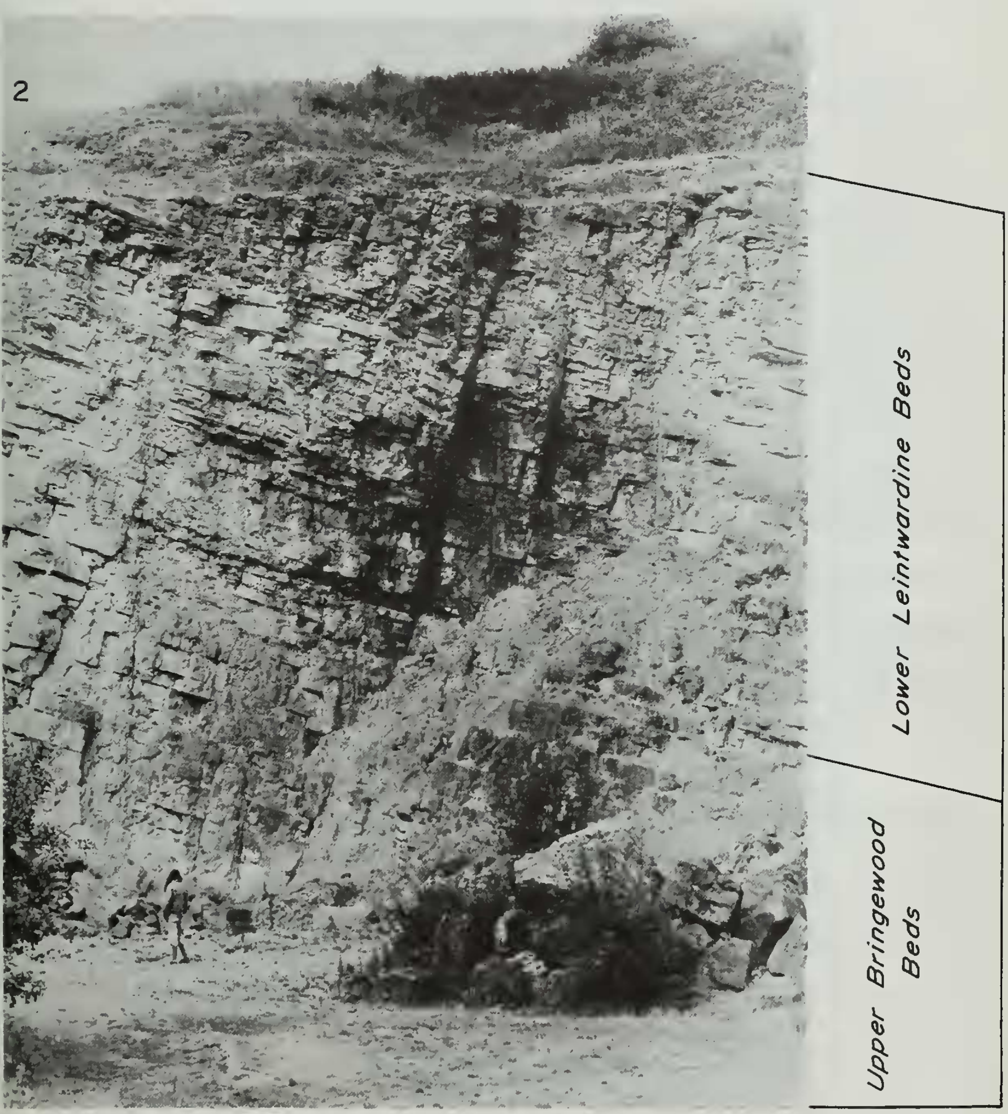
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Lower Leintwardine Beds
Upper Bringewood Beds

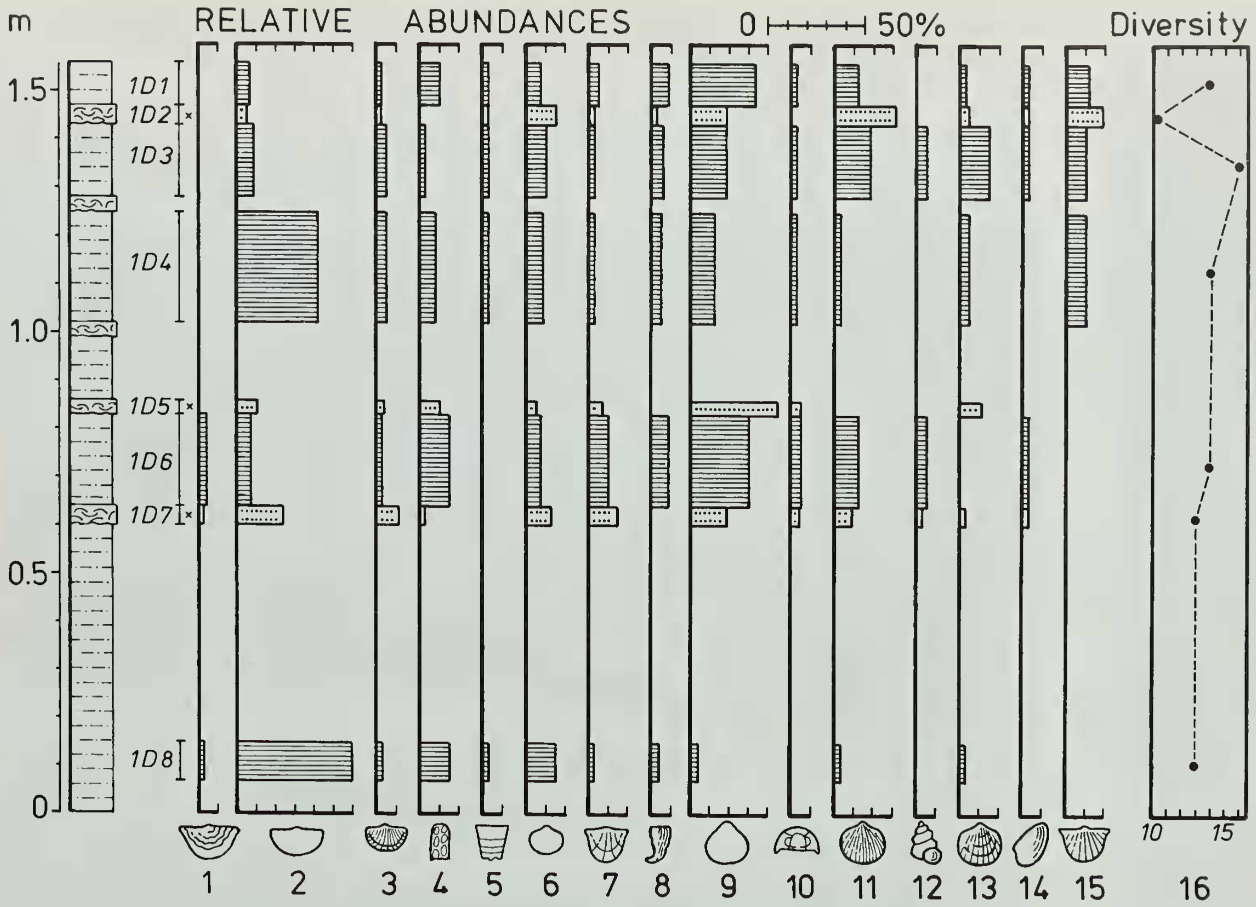


Fig. 5 Section 1D, Lower Bringewood Beds, Millichope, containing the *Mesopholidostrophia laevigata* Association. Shell beds are shown schematically, and occur within bioturbated siltstone. Note that transported assemblages from shell beds show no major faunal differences from disturbed neighbourhood assemblages in bioturbated siltstone. 1 – *Leptaena depressa* and *Lepidoleptaena* sp.; 2 – *Mesopholidostrophia laevigata*; 3 – *Amphistrophia funiculata*; 4 – bryozoa; 5 – cephalopods; 6 – various brachiopods; 7 – *Strophonella euglypha*; 8 – trochoid corals; 9 – *Gypidula lata*; 10 – trilobites; 11 – *Isorthis clivosa*; 12 – gastropods; 13 – *Atrypa reticularis*; 14 – bivalves; 15 – *Leptostrophia filosa*; 16 – rarefaction index for number of species at 50-individual sample size. Mean size of samples = 104 individuals.

Shell occurrence in the mudstone facies and laminated shale facies

Sections of the mudstone facies show a continuous stratigraphic occurrence of disturbed neighbourhood assemblages of shells. Shell material is evenly scattered through sediment in many orientations, as shown in Pl. 1, fig. 5. Rare lingulids and endobyssate bivalves remain in burrowing position, but life orientations and small-scale distributions of other forms have been destroyed by intense bioturbation. The pattern of long-term stratigraphic persistence of disturbed neighbourhood assemblages has been defined as the vital-pantostrate biofacies by Shäfer (1972). He considered the biofacies to preserve a complete in-place history of communities of fine-grained, quiet bottoms. This is corroborated in the mudstone facies by gradual stratigraphic cycles in the abundance of different species.

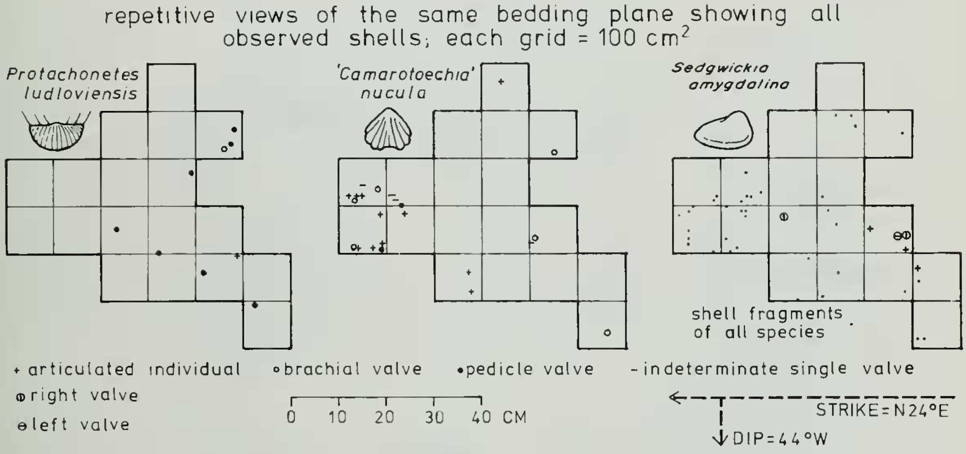


Fig. 6 Faunal variation in a disturbed neighbourhood assemblage of the *Protochonetes ludloviensis* Association in the Whitcliffe Beds of section 4A, Ledbury. This assemblage occurs 50·83 m above the base of the section, and can be located by this reading in Fig. 11.

The laminated shale facies contains rare intervals of intensely bioturbated sediment with a shell occurrence like that of the mudstone facies. Most of the laminated shale facies, however, contains only graptolites, cephalopods and other pelagic organisms, with very rare benthic shells. Shäfer (1972) discussed this type of shell occurrence as the letal-pantostrate biofacies, and related it to a poorly oxygenated bottom environment.

Shell occurrence in the bioturbated siltstone facies, calcisiltite facies and 'Aymestry Limestone' facies

Disturbed neighbourhood asemblages in bioturbated sediment are the main type of shell occurrence in these facies, and can be seen below the shell bed in Pl. 1, fig. 1. Transported assemblages occur as rare erosively-based shell beds, as also shown in Pl. 1, fig. 1. The fauna in transported shell beds does not differ from that in surrounding disturbed neighbourhood assemblages. This is shown graphically in Fig. 5, and discussed in the next section, p. 200.

Another type of transported assemblage consists of very thin bedding-parallel layers of closely-packed shells and shell fragments. A vertical section of one of these layers is shown in Pl. 1, fig. 3, and upper surfaces of layers are illustrated in Pl. 4, figs 1–5. These layers are often no thicker than a single shell, with no associated erosional surface, and have identical bioturbated sediment above and below. Shells are both whole and disarticulated, variably broken and unabraded. Faunal content is identical to surrounding disturbed neighbourhood assemblages. The shell layers probably represent 'swell lags', which are discussed below.

In general, shell occurrence in these three facies represents an intermediate taphonomic state between relatively in-place faunas of the underlying mudstone facies and more disturbed, often transported shell occurrences of the overlying coquinoid siltstone facies.

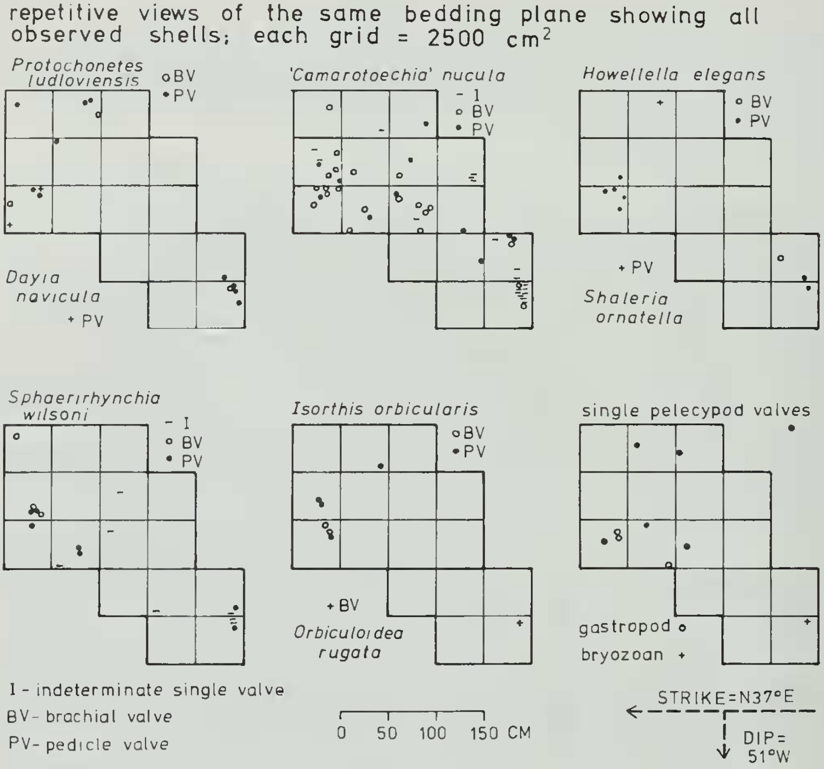


Fig. 7 Faunal variation in a disturbed neighbourhood assemblage of the *Sphaerirhynchia wilsoni* Association in the Lower Leintwardine Beds of section 4A, Ledbury. This plane is sample 4A42, which is shown stratigraphically in Fig. 10. The closely-packed shells in the two lower right grids are a small transported assemblage.

Shell occurrence in the coquinoid siltstone facies

Disturbed neighbourhood assemblages occur throughout bioturbated sediment of this facies, and have been investigated by inscribing grids on small areas of bedding surface. One example is shown in Fig. 6, where a discrete cluster of endobyssate bivalves occurs in one small area, separated by about 25 cm from a cluster of articulated and separate rhynchonellid valves. Both clusters are probably very close to their life positions, and their distributions suggest small-scale clumping of conspecific populations. Fig. 7 shows the distribution of a more scattered, disturbed neighbourhood assemblage. In this example, the slight differences in distribution of species may be a blurred reflection of original areas of life. However, the brachiopods are wholly disarticulated, and some species are represented mainly by pedicle valves.

Transported assemblages in the coquinoid siltstone facies are frequently represented by thin bedding-parallel layers of shells not associated with erosional surfaces. These are illustrated in Pl. 5, figs 1–4. Fig. 8 shows a grid analysis of faunal distribution in a thin layer of closely-packed shells. Significant lateral variation occurs in the composition of this shell layer. For example, Grid D in Fig. 8 contains a nearly equal mixture of '*Camarotoechia*', *Hyattidina*, *Salopina*, *Sphaerirhynchia* and *Isorthis*, while Grid K, 2 m away, is dominated by '*Camarotoechia*', *Salopina*, bivalves and ostracods. This small-scale variation may indicate that transport during formation of the shell layer was limited, partially maintaining original distributions. It probably does not result from different hydrodynamic properties of the various taxa, which would be nearly identical in the case of *Isorthis* and *Salopina*.

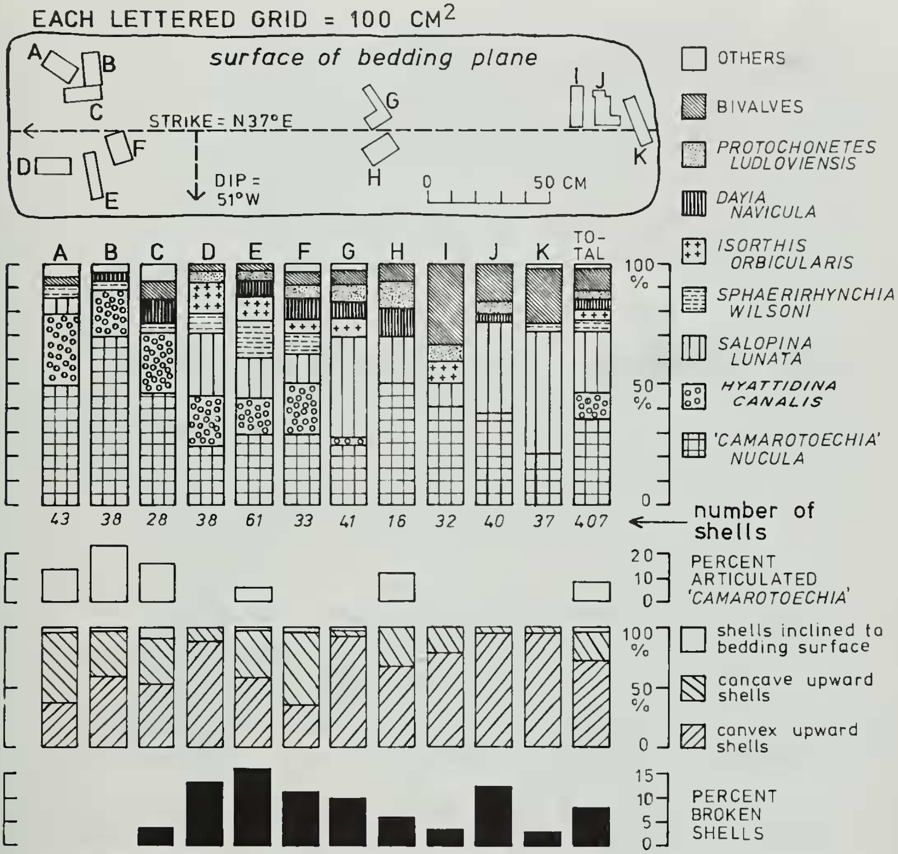


Fig. 8 Faunal variation in a very thin 'swell-lag' layer of transported shells, which covers the entire bedding plane and not just the sampled grids. This example is from the *Sphaerirhynchia wilsoni* Association of the Lower Leintwardine Beds, section 4A, and is shown in Fig. 10 as sample 4A45.

The swell lag mechanism discussed by Brenner & Davies (1973 : fig. 12) is a probable cause of the thin shell layers like that described above. Swell lags may form in fine-grained shelf sediment when storm-produced waves rework the upper shelf surface, suspending shells and sediment grains. Shells then settle first as a concentrated, coarse fraction, without significant lateral movement.

Storm-deposited beds of transported shells in the coquinoid siltstone facies have been described in the previous section, and are shown in Pl. 2, fig. 4. Faunal distribution on the upper surface of a shell bed is shown in Fig. 9. In contrast to the previous example, faunal content of the bed is fairly uniform over several metres, suggesting thorough mixing during transport. A graphic comparison of fauna between some transported shell beds and disturbed neighbourhood assemblages in the coquinoid siltstone facies is given in Figs 10 and 11. Faunal differences between the two types of assemblages and their implications will be discussed in the next section.

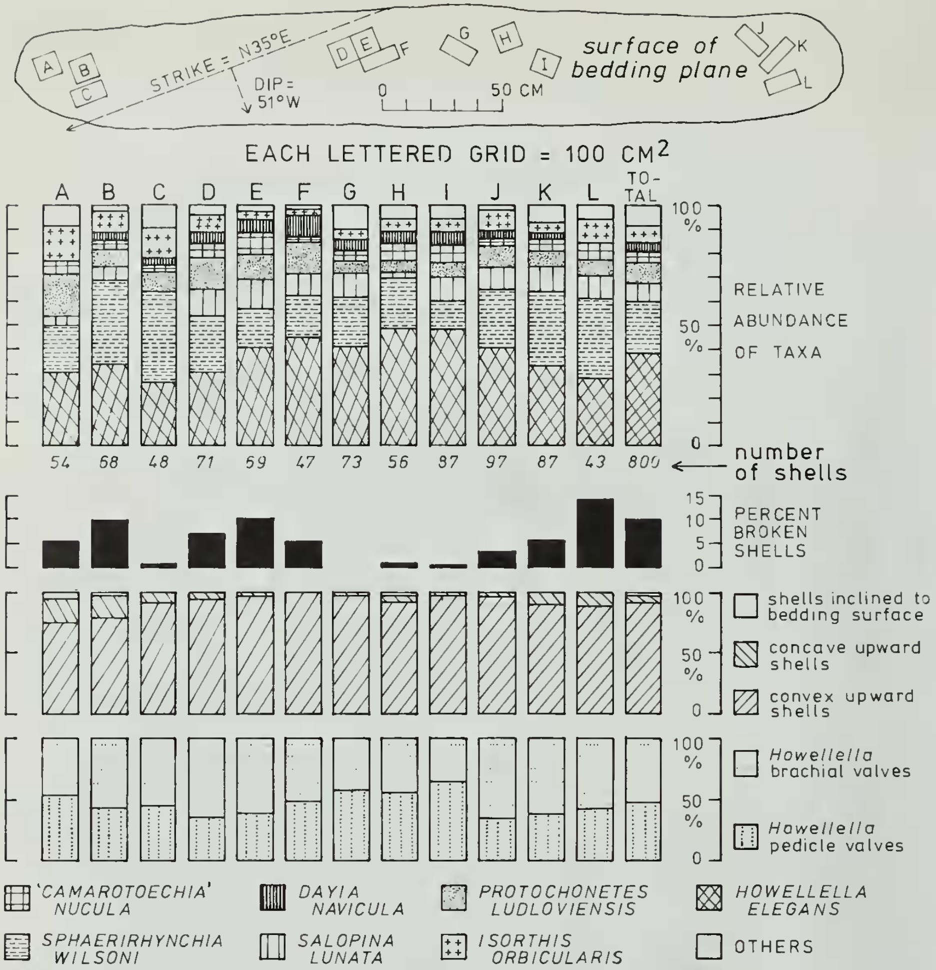


Fig. 9 Faunal variation on the upper surface of a 5 cm thick shell bed, shown as sample 4A44 in Fig. 10. From the *Sphaerirhynchia wilsoni* Association, Lower Leintwardine Beds, section 4A.

The alternation of transported and disturbed neighbourhood assemblages in the coquinoid siltstone facies represents the vital-lipostrate biofacies of Shäfer (1972). Nearly in-place communities are recorded in bioturbated sediment, biological information is lost at erosional surfaces, and transported faunas are introduced during storms. Shäfer's model for the vital-lipostrate biofacies states that benthic communities are killed *en masse* by very rapid storm sedimentation and erosion. This phenomenon affected faunas living during deposition of the coquinoid siltstone facies. Infaunal lingulids and bivalves occur in life position beneath storm-deposited, laminated siltstone sheets, and show no evidence of escape trails, while epifauna are found as concentrated, transported layers along the base of the sheets.

Analysis of shell transport

Method of analysis

This section analyses the effects of shell transport in the bioturbated siltstone facies and coquinoid siltstone facies. Transported assemblages have been identified on sedimentological not faunal

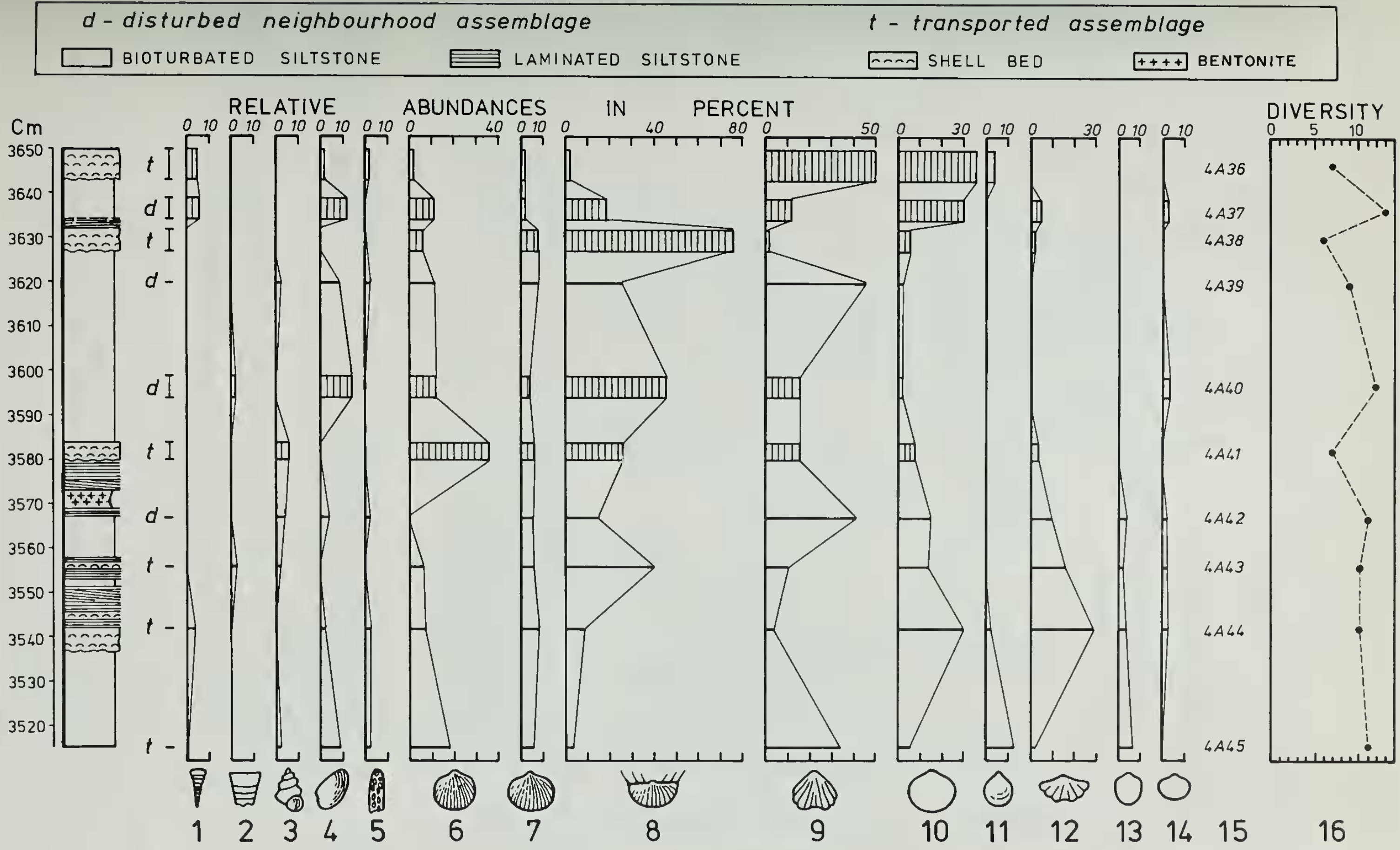


Fig. 10 Small-scale stratigraphic variation in the *Sphaerirhynchia wilsoni* Association, Lower Leintwardine Beds, section 4A, Ledbury, based on a mean count of 117 individuals per sample. Note the rarity of molluscs in transported assemblages. 1 – *Tentaculites tenuis* and *Cornulites serpularius*; 2 – cephalopods; 3 – *Cyclonema corallii*; 4 – bivalves; 5 – bryozoa; 6 – *Salopina lunata*; 7 – *Isorthis orbicularis*; 8 – *Protochonetes ludloviensis*; 9 – '*Camarotoechia*' *nucula*; 10 – *Sphaerirhynchia wilsoni*; 11 – *Hyattidina canalis*; 12 – *Howellella elegans*; 13 – *Dayia navicula*; 14 – other brachiopods; 15 – sample numbers; 16 – rarefaction index for number of species at 50-individual sample size.

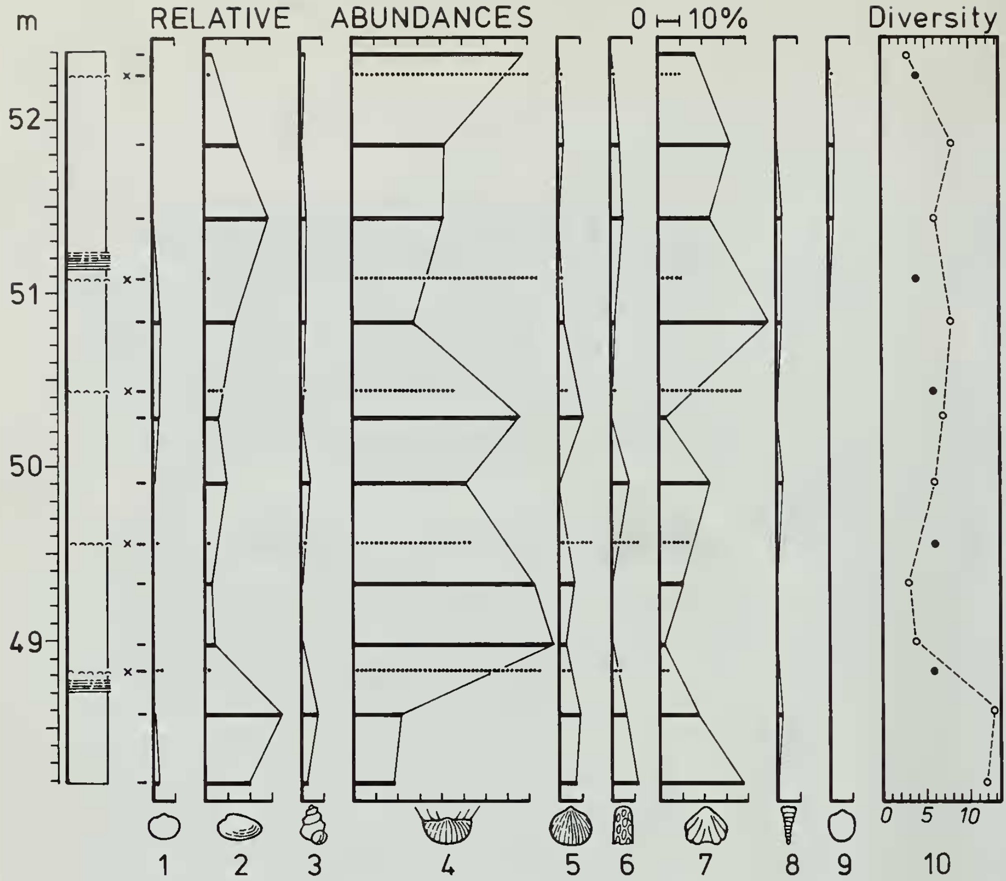


Fig. 11 Faunal comparison of transported assemblages (dotted bars) and disturbed neighbourhood assemblages (solid bars) in the *Protochonetes ludloviensis* Association, Whitcliffe Beds, section 4A, Ledbury, based on mean count of 89 individuals per sample. 1 – various brachiopods; 2 – bivalves; 3 – gastropods; 4 – *Protochonetes ludloviensis*; 6 – bryozoa; 7 – '*Camarotoechia*' *nucula*; 8 – *Cornulites serpularius* and *Serpulites longissimus*; 9 – *Dayia navicula*; 10 – rarefaction index for number of species at 50-individual sample size (solid circles = transported assemblages).

grounds, as explained in the two previous sections. Based on this, the faunal characteristics of transported assemblages are empirically described and compared with the fauna of disturbed neighbourhood assemblages. This establishes some relative effects of shell transport among Ludlow shelf faunas of the study area.

Comparisons between the two types of assemblage were made with a simple 2 × 2 contingency test (for example, number of bivalves versus number of brachiopods in transported assemblages and disturbed neighbourhood assemblages). Data and χ^2 values are given in Tables 6–12.

Articulation of brachiopods

Brachiopods with resorbtion in the tooth-socket structure show locally high rates of articulation in all sedimentary facies, with up to 60% of specimens occurring as whole shells in some samples. For brachiopods without resorbtion in the tooth-socket structure, a maximum of 20% articulated specimens occurs in the mudstone facies. Articulation of these types of brachiopods significantly decreases from the mudstone facies to the bioturbated siltstone facies and coquinoid siltstone facies, which may result from more agitated conditions of sediment deposition. This relation is shown for *Isorthis* and *Howellella* in Table 6.

Table 6 Articulation data for two deltidiodont brachiopods; note the continuous stratigraphic trends. c – coquinoid siltstone facies; b – bioturbated siltstone facies; m – mudstone facies; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association; Go – *G. obovata* Association; LLB – Lower Leintwardine Beds; LBB – Lower Bringewood Beds; MEB – Middle Elton Beds

facies	association	whole shells	separate valves	per cent articulated	stratigraphic unit
Isorthis clivosa and *I. orbicularis*					
c	upSw	11	372	2·9	LLB
b	lpSw	13	270	4·6	LBB
b	Ml	89	1349	6·2	LBB
m	Go	483	2043	23·7	MEB
Howellella elegans					
c	upSw	3	304	1·0	LLB
b	Ml	18	518	3·4	LBB
m	Go	34	216	13·6	MEB

Table 7 Comparison of articulation between disturbed neighbourhood assemblages and transported assemblages for selected brachiopods. Pl – *P. ludloviensis* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association

association	assemblage type	whole shells	separate valves	χ^2	significant difference?
Isorthis orbicularis					
upSw	disturbed neighbourhood	11	372	1·4	no
	transported	3	216		
lpSw	disturbed neighbourhood	13	270	0·7	no
	transported	3	105		
Salopina lunata					
Pl	disturbed neighbourhood	41	486	11	yes
	transported	26	713		
upSw	disturbed neighbourhood	7	190	6	yes
	transported	3	398		
Howellella elegans					
upSw	disturbed neighbourhood	3	304	2·5	no
	transported	1	521		
lpSw	disturbed neighbourhood	11	867	1·6	no
	transported	5	773		
'*Camarotoechia*' *nucula*					
Pl	disturbed neighbourhood	386	1088	18	yes
	transported	94	451		
upSw	disturbed neighbourhood	118	716	24	yes
	transported	42	622		

Comparison of brachiopod articulation between disturbed neighbourhood and transported assemblages indicates that transport on the Ludlow shelf related variably to further disarticulation of shells. Within transported assemblages, there is a significant reduction in articulated shells of *Salopina* and '*Camarotoechia*' (Table 7). However, no significant difference in articulation of *Isorthis* and *Howellella* is shown between transported and disturbed neighbourhood assemblages (Table 7).

Valve sorting of brachiopods

There is a preponderance of pedicle valves in Orthida, Strophomenida, Pentamerida and some Spiriferida in all Ludlow shelf facies. This is a very general phenomenon among Silurian faunas, and has also been noted by Ziegler *et al.* (1968*a*). The scale of this relation cannot be explained by local sedimentary sorting, and must involve greater susceptibility of brachial valves to mechanical and biological destruction.

In Ludlow sediments, sorting of valves in disturbed neighbourhood assemblages will be considered as the original sample drawn upon to produce valve ratios in transported assemblages. Differences between the two assemblage types can be assigned to the effects of any additional sorting during transport. Data in Table 8 show that transport may or may not involve valve sorting relative to valve ratios encountered in disturbed neighbourhood assemblages. Where further sorting occurs, it usually involves increased abundance of brachial valves in transported assemblages. Transported *Isorthis*, *Salopina* and *Protochonetes* show a closer approach to unity of the ratio of number of pedicle to brachial valves than in disturbed neighbourhood assemblages

Table 8 Comparison of valve sorting between disturbed neighbourhood assemblages and transported assemblages for selected brachiopods. Designations for associations as in Table 7

association	assemblage type	pedicle valves	brachial valves	χ^2	significant difference?
Isorthis orbicularis					
upSw	disturbed neighbourhood	223	149	30	yes
	transported	79	137		
lpSw	disturbed neighbourhood	175	95	9	yes
	transported	50	55		
Salopina lunata					
Pl	disturbed neighbourhood	277	209	0·2	no
	transported	396	317		
upSw	disturbed neighbourhood	131	59	15	yes
	transported	208	190		
Protochonetes ludloviensis					
Pl	disturbed neighbourhood	1772	454	0·06	no
	transported	1426	358		
upSw	disturbed neighbourhood	174	37	8	yes
	transported	216	86		
'*Camarotoechia*' *nucula*					
Pl	disturbed neighbourhood	432	488	0·1	no
	transported	187	212		
upSw	disturbed neighbourhood	198	308	1·6	no
	transported	196	258		

(Table 8). Rapid transport and permanent burial of brachial valves of these taxa possibly protected them from forms of mechanical or biological destruction operative in disturbed neighbourhood assemblages.

Breakage of brachiopod shells

Within disturbed neighbourhood assemblages, 10% of brachiopod shells and valves show primary non-compactional breakage in the mudstone facies, 21% are broken in the bioturbated siltstone facies and 5% are broken in the coquinoid siltstone facies. These differences are highly significant (Table 9). Greatest proportion of breakage in the two distal shelf, low-energy facies suggests long-term exposure of the shells at the sediment surface, and their continued disturbance by burrowers. In the coquinoid siltstone facies, shells were probably buried more rapidly and permanently, and protected from a great amount of breakage. Broken edges of shells in all facies are unabraded, and surface ornament is also sharply preserved.

Table 9 Primary, non-compactional shell breakage in Ludlow brachiopods. c – coquinoid siltstone facies; b – bioturbated siltstone facies; m – mudstone facies; Pl – *P. ludloviensis* Association; Sw – *S. wilsoni* Association; Ml – *M. laevigata* Association; Go – *G. obovata* Association

facies	association	section	assemblage type	broken shells	whole shells	χ^2	significant difference?
c	Pl	2B, 2C	disturbed neighbourhood	40	674	85	yes
b	Sw, Ml	3A	disturbed neighbourhood	296	1109		
c	Pl	2B, 2C	disturbed neighbourhood	40	674	12	yes
m	Go	51	disturbed neighbourhood	252	2338		
c	Pl	2B, 2C	disturbed neighbourhood	40	674	0·4	no
c	Pl	2B, 2C	transported	34	671		
c	Pl	5B, 5C	disturbed neighbourhood	19	352	0·8	no
c	Pl	5A	transported	9	239		
b	Sw, Ml	3A	disturbed neighbourhood	296	1109	23	yes
b	Sw, Ml	3A	transported	94	655		

In the bioturbated siltstone facies, transported assemblages contain a significantly lower proportion of broken shells than do disturbed neighbourhood assemblages (Table 9). There is no significant difference in shell breakage proportion between the two assemblage types in the coquinoid siltstone facies (Table 9). Transport of shells on the Ludlow shelf does not appear to have contributed to shell breakage, probably because it was of a turbidity current type, as discussed later. This emphasizes that the shell breakage which does occur is probably a result of prolonged exposure under low-energy conditions.

Infauna – epifauna relations

Of 104 *Lingula* collected from the bioturbated siltstone facies and coquinoid siltstone facies, only one specimen has been found in a transported shell bed assemblage. The same relation is shown by bivalves, which were probably all infaunal or semi-infaunal, except for *Palaeopecten danbyi*. Table 10 shows the proportions of infaunal bivalves to epifaunal brachiopods in several communities from the two facies. Bivalves are significantly concentrated in disturbed neighbourhood assemblages, and are very poorly represented in transported assemblages. This relation is also shown in stratigraphic diagrams in Figs 10–11, pp. 201–2. It indicates that storm events on the Ludlow shelf carried and concentrated epifauna, while leaving infauna relatively unaffected. Another taphonomic consequence of this phenomenon is lower species diversity of transported assemblages relative to disturbed neighbourhood assemblages (Fig. 11).

Table 10 Comparative abundance of articulate brachiopods and bivalves between disturbed neighbourhood assemblages and transported assemblages. χ^2 tests between assemblage types within each association show a significant concentration of bivalves in disturbed neighbourhood assemblages. Pl – *P. ludloviensis* Association; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association

association	assemblage type	articulate brachiopod individuals	bivalve individuals	bivalves as % of total
Pl	disturbed neighbourhood	3250	408	11·1
Pl	transported	2254	41	1·8
So	disturbed neighbourhood	694	68	8·9
So	transported	434	11	2·5
upSw	disturbed neighbourhood	1779	104	5·5
upSw	transported	2463	44	1·7
lpSw	disturbed neighbourhood	2281	63	2·7
lpSw	transported	1011	9	0·9

Life habit groups of brachiopods

Different life habit groups of brachiopods appear to show variable susceptibility to transport. Three major groups are considered in the following discussion.

1. Pedically-attached brachiopods, which include all forms not included in the following two groups.
2. Strophomenida, which were mainly unattached.
3. Reclining brachiopods, which lived with the beaks inclined into the sediment and the commissure oriented upwards. Pedicle attachment was weak or absent, and posterior weighting of the shell held individuals in place.

Table 11 Comparative abundance of reclining and pedunculate brachiopods (as defined in text) between disturbed neighbourhood and transported assemblages. c – coquinoid siltstone facies; b – bioturbated siltstone facies; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association

facies	association	assemblage type	reclining	pedunculate	χ^2	significant difference?
c	So	disturbed neighbourhood	161	327	17	yes
		transported	23	126		
c	upSw	disturbed neighbourhood	350	1214	244	yes
		transported	1041	1161		
b	lpSw	disturbed neighbourhood	972	1062	109	yes
		transported	276	716		
b	Ml	disturbed neighbourhood	149	76	1·2	no
		transported	90	58		

Data comparing pedunculate and reclining brachiopods are given in Table 11. In the coquinoid siltstone facies, reclining forms are dominated by *Sphaerirhynchia*, *Hyattidina* and *Dayia*, and are significantly concentrated in transported assemblages. No significant concentration, however, is apparent in the bioturbated siltstone facies. Comparisons of pedunculate brachiopods and Strophomenida show no difference in distribution in the bioturbated siltstone facies, but a significant concentration of Strophomenida in transported assemblages of the coquinoid siltstone facies (Table 12). These results might reflect lack of attachment and easier susceptibility to movement of reclining brachiopods and Strophomenida.

Table 12 Comparative abundance of strophomenide and pedunculate brachiopods between disturbed neighbourhood assemblages and transported assemblages. c – coquinoid siltstone facies; b – bioturbated siltstone facies; Pl – *P. ludloviensis* Association; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association

facies	association	assemblage type	strophomenide	pedunculate	χ^2	significant difference ?
c	Pl	disturbed neighbourhood	1813	1420	31	yes
		transported	1431	821		
c	So	disturbed neighbourhood	306	327	44	yes
		transported	285	126		
c	upSw	disturbed neighbourhood	210	1214	7	yes
		transported	265	1161		
b	lpSw	disturbed neighbourhood	247	1062	111	yes
		transported	19	716		
b	Ml	disturbed neighbourhood	168	76	1·5	no
		transported	163	58		

Community integrity of transported assemblages

The stratigraphic profiles of fauna constructed in this study clearly indicate that transported shell beds in Ludlow sediments contain the same communities as adjacent disturbed neighbourhood assemblages, apart from the relations discussed above. The sequence from the bioturbated siltstone facies to coquinoid siltstone facies (Lower Bringewood Beds to Whitcliffe Beds) contains six benthic communities in ascending stratigraphic order, as shown in Fig. 12. Within the stratigraphic interval of occurrence in each of these six communities there are beds of transported shells, but in no observed case do these beds include an ecologically mixed or disjunct fauna. The basic community integrity of transported assemblages can be seen in the faunal profiles shown in Figs 16–20 (pp. 213–8), where such samples are indicated with an ‘ × ’.

Summary and general implications of shell transport

Comparison of disturbed neighbourhood and transported assemblages in Ludlow shelf sediments produces the following conclusions regarding the effect of shell transport.

1. Minor contribution to disarticulation and concentration of brachial valves in some brachiopods.
2. No effect in shell breakage.
3. Concentration of epifauna, with very little effect upon infauna.
4. Selective removal and concentration of certain strophomenides and reclining brachiopods in the coquinoid siltstone facies.
5. No mixing of benthic community elements.

According to the storm-related model of shelf sedimentation presented in the sedimentology section, most transport of Ludlow shells occurred in association with very rapid turbidity currents. During storms, shells were probably incorporated and partially suspended in rapidly-moving ‘clouds’ of suspended silt, finally settling as coarse basal layers with reduction of the current strength. This form of transport would explain the lack of infauna, concentration of epifauna and lack of abrasion and shell breakage in transported assemblages. It could result in the movement of shells for kilometres across the shelf without mechanical damage. Reineck & Singh (1973) have noted the long-range transport of living *Hydrobia* in North Sea storm sedimentation.

Nevertheless, shell transport during Ludlow storm sedimentation did not mix different communities. Although differing in quantitative details, transported assemblages are similar in content of epifaunal species to adjacent disturbed neighbourhood assemblages. When an ecological change from one community to another occurs in bioturbated parts of a stratigraphic section, there is a corresponding change in transported faunas, indicating a contemporaneous change in the *source* of transported shells.

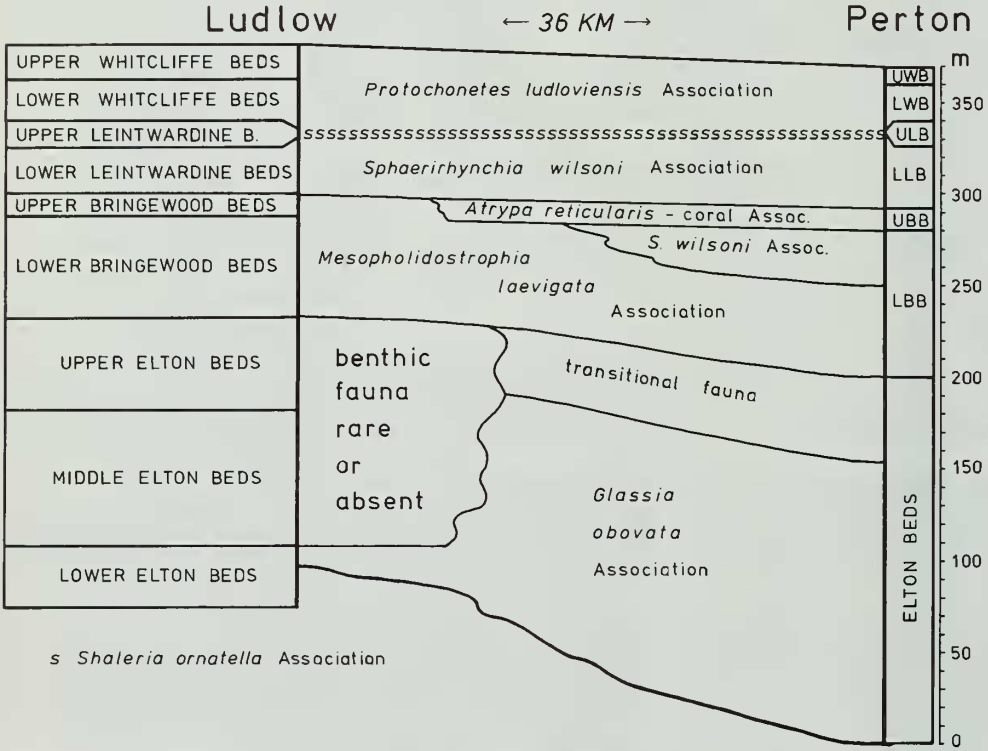


Fig. 12 Generalized cross-section showing stratigraphic relations of benthic communities described in text.

One explanation is that shell transport may have occurred over a distance of only metres or less. This is possible on the distal fringe of a mass-deposited sheet of silt, or in the case of swell lags discussed earlier, but it is not a suitable general explanation for the abundant shell beds in the Ludlow sections. Another possibility is that the Ludlow communities of the Welsh Borderland synchronously occupied such wide expanses of shelf that transport over distances of kilometres would not introduce mixed or disjunct faunas into the areas studied. This explanation is supported by the correlations of Holland *et al.* (1963) and the discussion given in the stratigraphy section.

Community definition

The transect method of community definition

A descriptive recognition of past associations of organisms must precede their biological or dynamic interpretation. For this purpose, the community definition of Ehrlich *et al.* (1973) will be used. 'The organisms existing at a particular place and time may be called a *community*. The word has no special biological meaning, it is merely a useful descriptive term.' Petersen (1918) showed that particular combinations of benthos occupy discrete areas of seafloor, and can be mapped. One can thus define a community by specifying either faunal composition or areal boundaries interchangeably.

Jurgen Dörjes has applied a transect method to the areal definition of modern marine benthic communities (Dörjes *et al.* 1969, 1970; Dörjes 1971, 1972). An example of this work is reproduced in Fig. 13. Samples are taken along a line across a known environmental gradient, usually perpendicular to a coastline and boundaries of sedimentary facies. The transect line is drawn on paper, and occurrences of species are plotted along it according to sample to produce a graphic profile of faunal distribution. The profiles are then divided into contiguous segments which define communities, according to distinctive overlaps of species ranges along the line of transect (Fig. 13).

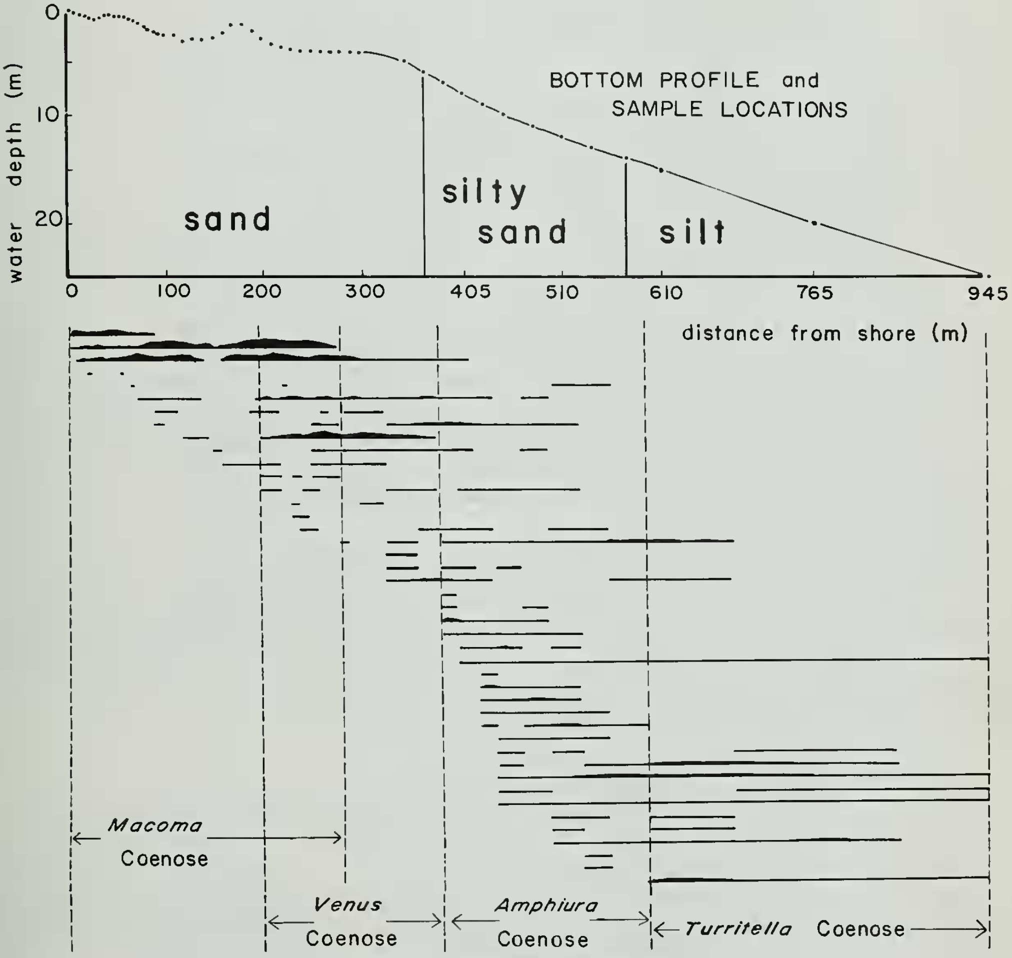


Fig. 13 Distribution of mollusc species along a sedimentary-bathymetric gradient in the Gulf of Gaeta, Italy, illustrating the transect method of defining communities. Modified from Dörjes (1971 : fig. 5).

The transect method provides a direct picture of community boundaries and gradations, and eliminates the need for statistical comparison of scattered samples. Some community boundaries represent very sharp changes in faunal composition, as where sand shoals border mud-filled troughs (Dörjes 1972 : pl. 2). In other transects, the faunas of communities grade into one another along continuous transitions of sediments (Fig. 13). This phenomenon, where community gradations reflect environmental gradients, has also been discussed by Johnson (1972).

Application of the transect method to stratigraphic sections

The transect method for defining benthic communities has been applied to stratigraphic sections in the Welsh Borderland according to the sampling methods described (p. 178). Stratigraphic sections have been treated primarily as an environmental rather than purely a time gradient, following the succession of sedimentary facies described earlier. Faunal distribution along the stratigraphic gradient of environments is used to define benthic communities.

Faunal composition at each sampling point along the measured sections has been plotted according to the relative abundances of individuals of each constituent taxon. Histograms for each taxon, arranged in stratigraphic order, are then joined by lines to form a continuous stratigraphic profile of its abundance. The resulting diagrams, or 'faunal profiles', for measured sections are grouped as in Figs 16–21. Along with the statistics in Appendix 3 (pp. 262–74), they constitute the basic source for community definitions.

Several important points must be noted concerning the faunal profiles in Figs 16–21:

1. A key to symbols in the profiles is given in Figs 14 and 15.
2. Very low relative abundances have been exaggerated to values of 3 or 5% to be visible in the diagrams. The total relative abundances shown for each sample thus often exceed 100%.
3. Samples of fewer than 30 individuals were not plotted, so that the average sampling error for a relative abundance shown is less than 5% (see Appendix 2, p. 260).
4. Most samples are of 50–100 individuals, and the absence of any given species from a sample may be an artefact of insufficient sampling (Appendix 2). However, the continued absence of a species from several samples in stratigraphic succession is evidence for genuine non-occurrence. Representative sample sizes used for the faunal profiles are given in Tables 17–20 in Appendix 3.
5. Profiles of diversity give the number of species at 50-individual sample size, based on both direct count and the rarefaction method of Sanders (1968). In samples with abundant bryozoa, these diversity measurements are conservative, as this group was not given species-level study in thin section.
6. The faunal profiles are compilations from the more complete set of basic data given in Appendix 3. Relative abundances of species other than brachiopods are combined in the faunal profiles according to phylum or class because of low abundances and the sporadic occurrence of most individual species. This has been done as a matter of convenience in constructing the diagrams, and does not indicate that the non-brachiopod groups have been omitted from the community analysis. The species-level data for molluscs, trilobites and minor groups in the Ludlow sections is summarized in Appendix 3.

Definition of the Ludlow shelf communities

Following the transect method, Ludlow communities are defined, spatially, as stratigraphically successive portions of the faunal profiles. Community boundaries were chosen by inspection of the stratigraphic ranges and changes in abundance of taxa, and are designated as dotted lines across the faunal profiles, perpendicular to the stratigraphic column. Several examples of these boundaries can be seen in Figs 16 and 17. In most cases, the nature of a faunal change permits the unequivocal location of an ecological boundary within a 2–5 m stratigraphic interval. The significance of this is discussed later.

The benthic communities recognized here are designated with the formal term 'Association', preceded by the name of one of their species, and the terms 'community' and 'association' are used interchangeably throughout the text. It must be re-emphasized that these 'Associations' are defined on a spatial basis, as the total fauna in a designated stratigraphic interval. They are not defined or intended to be recognized by some specific numerical combination of taxa. A stratigraphic summary of all the associations defined in the measured sections is shown in Fig. 12, p. 208.

Glassia obovata Association

The *Glassia obovata* Association is restricted to the Elton Beds, where it occurs throughout the mudstone facies and in minor bioturbated intervals within the laminated shale facies. Small brachiopods, bivalves and trilobites are the dominant forms, and although species content is relatively constant throughout the areas studied, relative abundances of different groups show significant variations from one section to another. Stratigraphic profiles of this community are given in Figs 19, 21, 22 and 23, and checklists of species are given in Appendix 3, Tables 15 and 17.

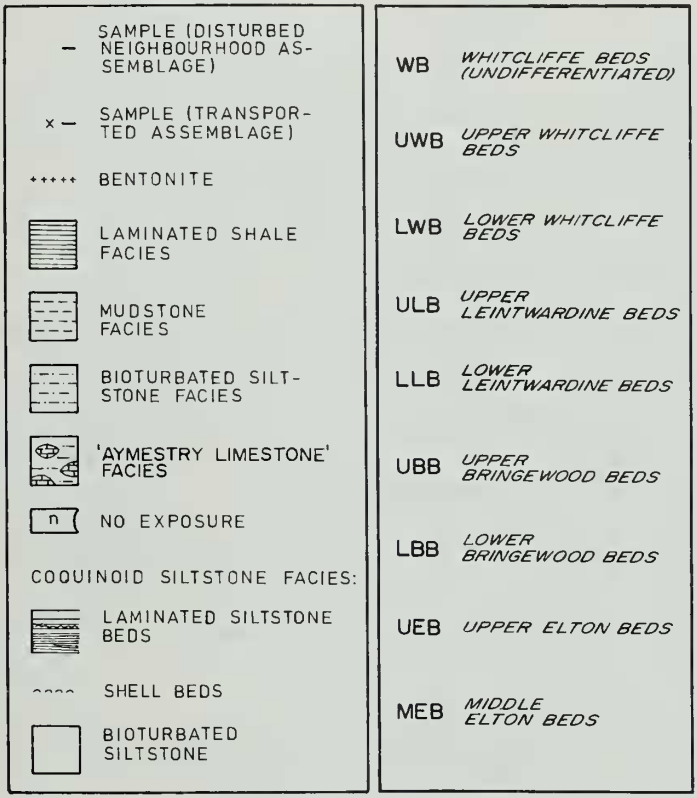


Fig. 14 Standard symbols used in stratigraphic columns in Figs 16–22.

Brachiopods

The most abundant brachiopod occurring in the *G. obovata* Association is the strophomenide *Aegiria grayi*, which is less than 5 mm in size and reaches local densities of 18 000 shells per square metre. *Aegiria grayi* is listed by sample in Appendix 3, but it is not included in calculations or faunal profiles for this community, as it appears to have possessed an epiplanktic mode of life. The main evidence for this is its presence in laminated mudstones of the shelf edge and basin areas in association with a wholly pelagic fauna of graptolites, small orthoconic nautiloids and praecardiacean bivalves. *Aegiria grayi* also appears in association with a pelagic graptolitic fauna in the Upper Leintwardine Beds, again with a distribution centred in the basin and shelf edge (Holland & Lawson 1963). An epiplanktic mode of life for the related Ordovician genera *Sericoidea* and *Chonetoidea* has been shown by Bergström (1968) and Havlíček (1967).

Thirty other brachiopod species have been recorded from the *G. obovata* Association. These species comprise 85% of individuals in the association, and most are below 15 mm in size. One characteristic pattern of brachiopod occurrence is shown in Fig. 22, p. 220. In this example, a variety of species and adaptive types are present in fairly equitable abundances, with continuous and relatively constant densities of shells in the vertical profile of bioturbated mudstone. Each species shows gradual long-term changes in abundance. These cycles are discussed in detail later, and related to optimal periods of larval recruitment. Although the content of brachiopod species in the association remains relatively constant, the cycles of each species' abundance produce subtle and continuous fluctuations in community composition through time.

Fig. 15 Standard symbols used for species and other taxa in Figs 16–23, 25.

Another pattern of brachiopod occurrence is seen near Perton (Fig. 21, p. 219), where *Isorthis clivosa* and *Glassia obovata* greatly predominate over other brachiopods, and comprise most individuals in the association as a whole. In *Isorthis clivosa*, these fluctuations range through abundances of about 20–80% of the entire shelled fauna, and occur as predictable cycles occupying stratigraphic intervals of 3–7 m. *Glassia obovata* shows a much more erratic stratigraphic pattern, and dense concentrations of articulated individuals come and go suddenly within the vertical profile of bioturbated mudstone (Fig. 21). Species diversity is low where these two forms predominate, and other brachiopods occur sporadically and seldom exceed 10% of individuals per sample.

Parastrophinella sp. is a small plicate pentameracean which plays a minor role in the brachiopod occurrences discussed above. In the laminated shale facies, however, it becomes the most abundant brachiopod of the association (Fig. 23, p. 221). Relatively few brachiopod species of the *G. obovata* Association extend from the mudstone facies to the laminated shale facies.

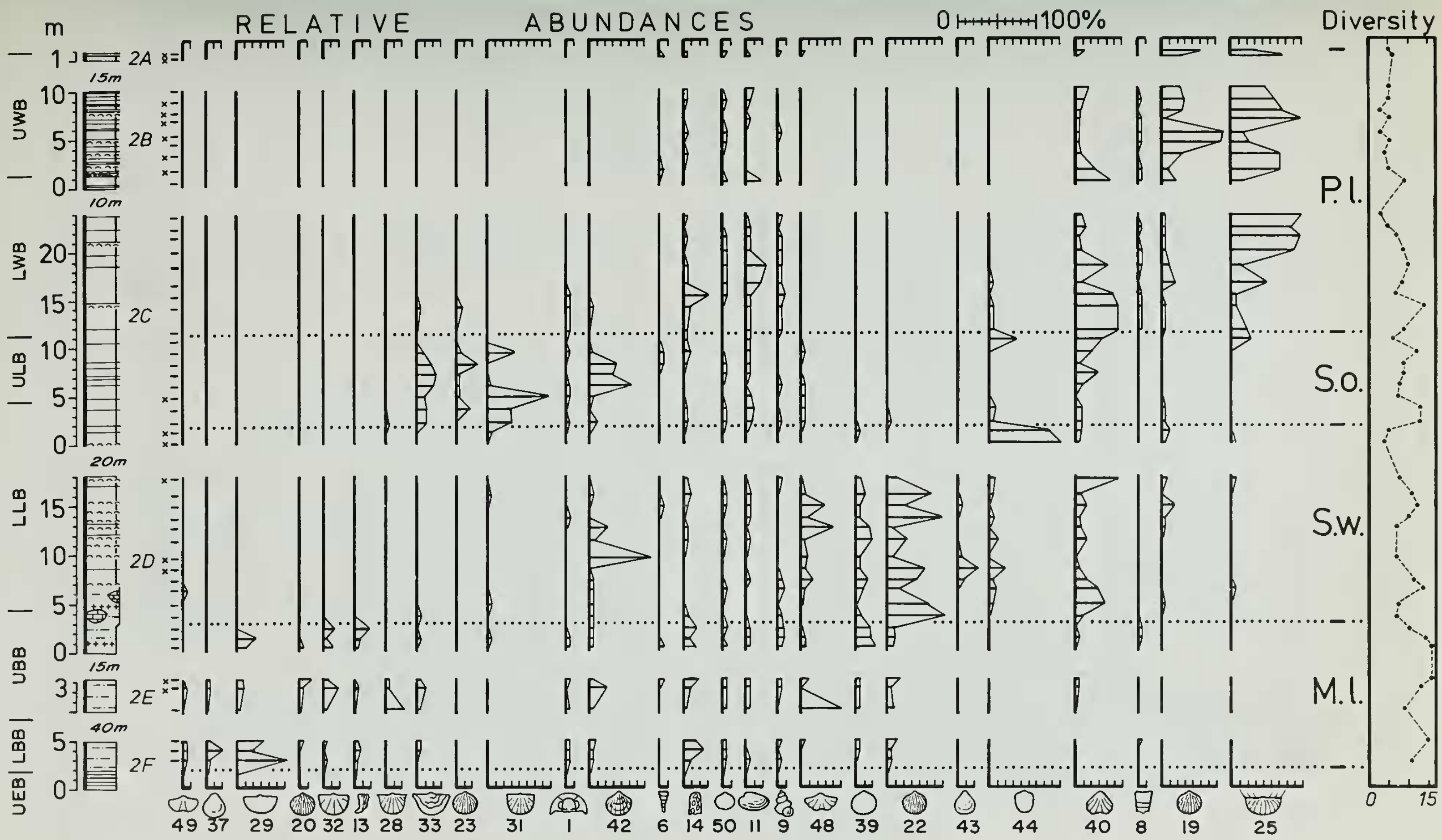


Fig. 16 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw) and *Mesopholidostrophia laevigata* Association (Ml) in the Ludlow area. All sections except 2E contain the type stratigraphic boundaries designated by Holland *et al.* (1963). Symbols are explained in Figs 14 and 15. The diversity scale gives the rarefaction index for number of species at 50-individual sample size.

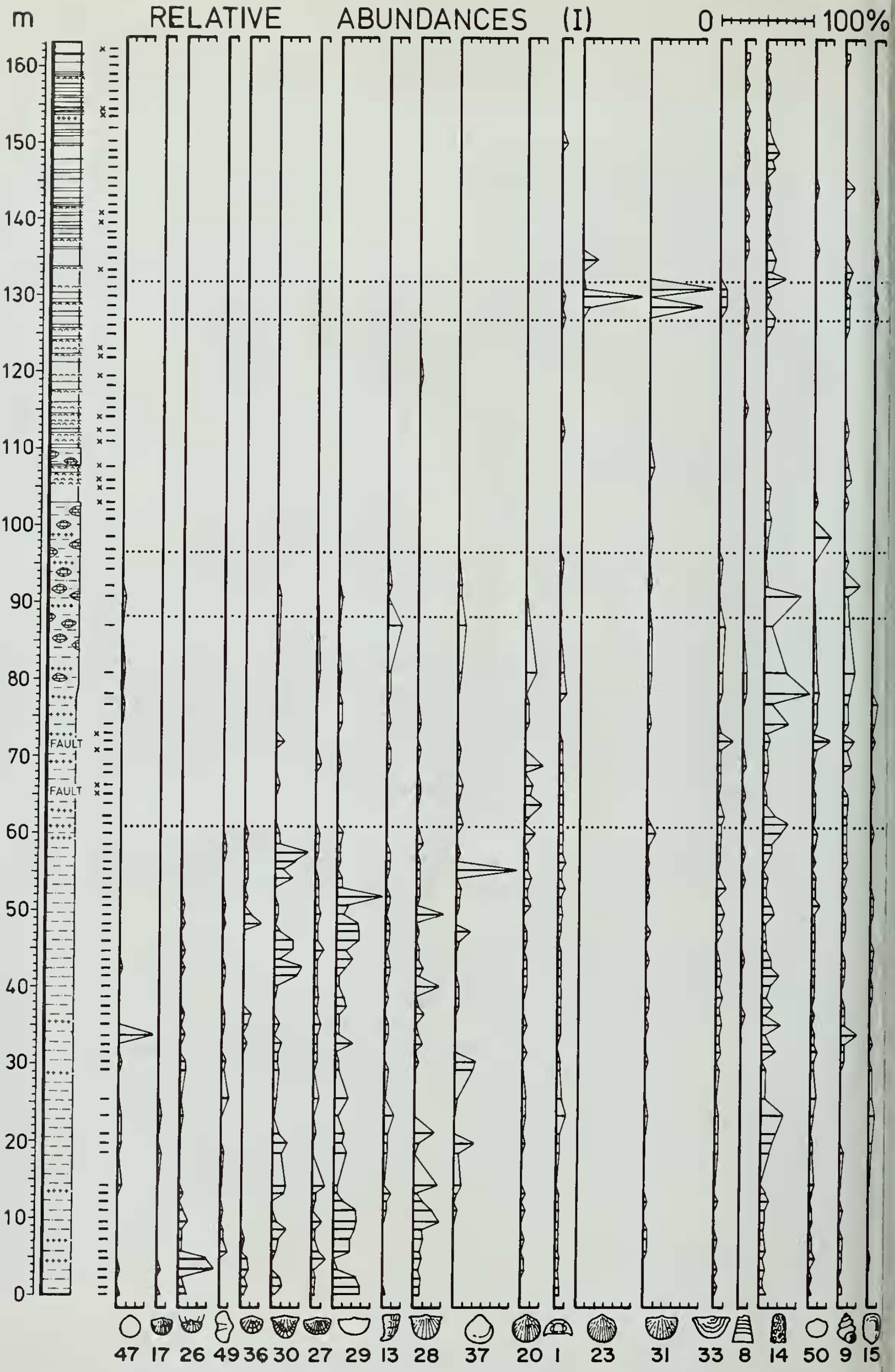
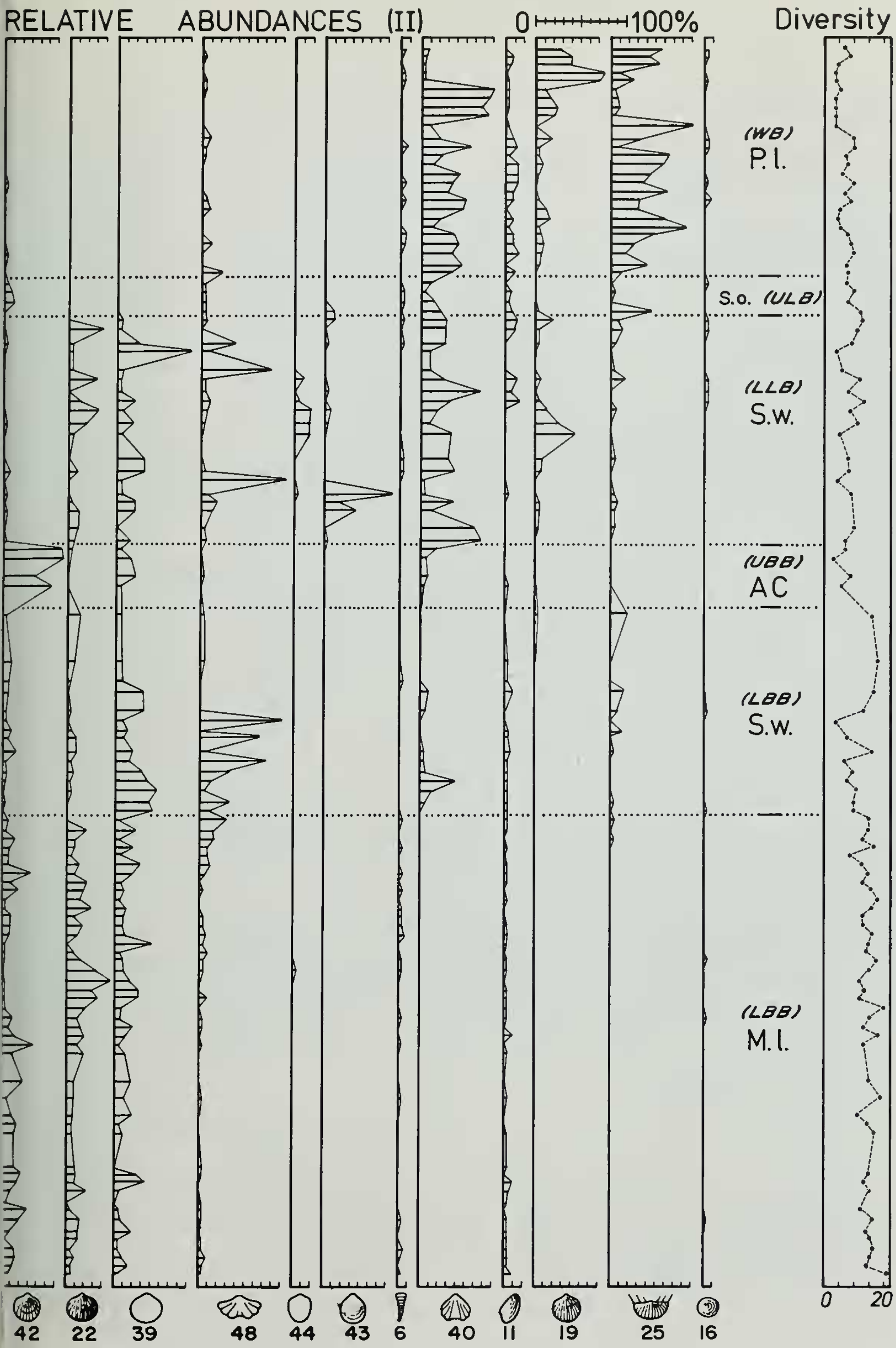


Fig. 17 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *laevigata* Association (Ml) in section 3A, Woodbury Quarry. Symbols are explained in Figs 14 and



phaerirhynchia wilsoni Association (Sw), *Atrypa reticularis* – coral Association (AC), and *Mesopholidostrophia*
5. The diversity scale gives the rarefaction index for number of species at 50-individual sample size.

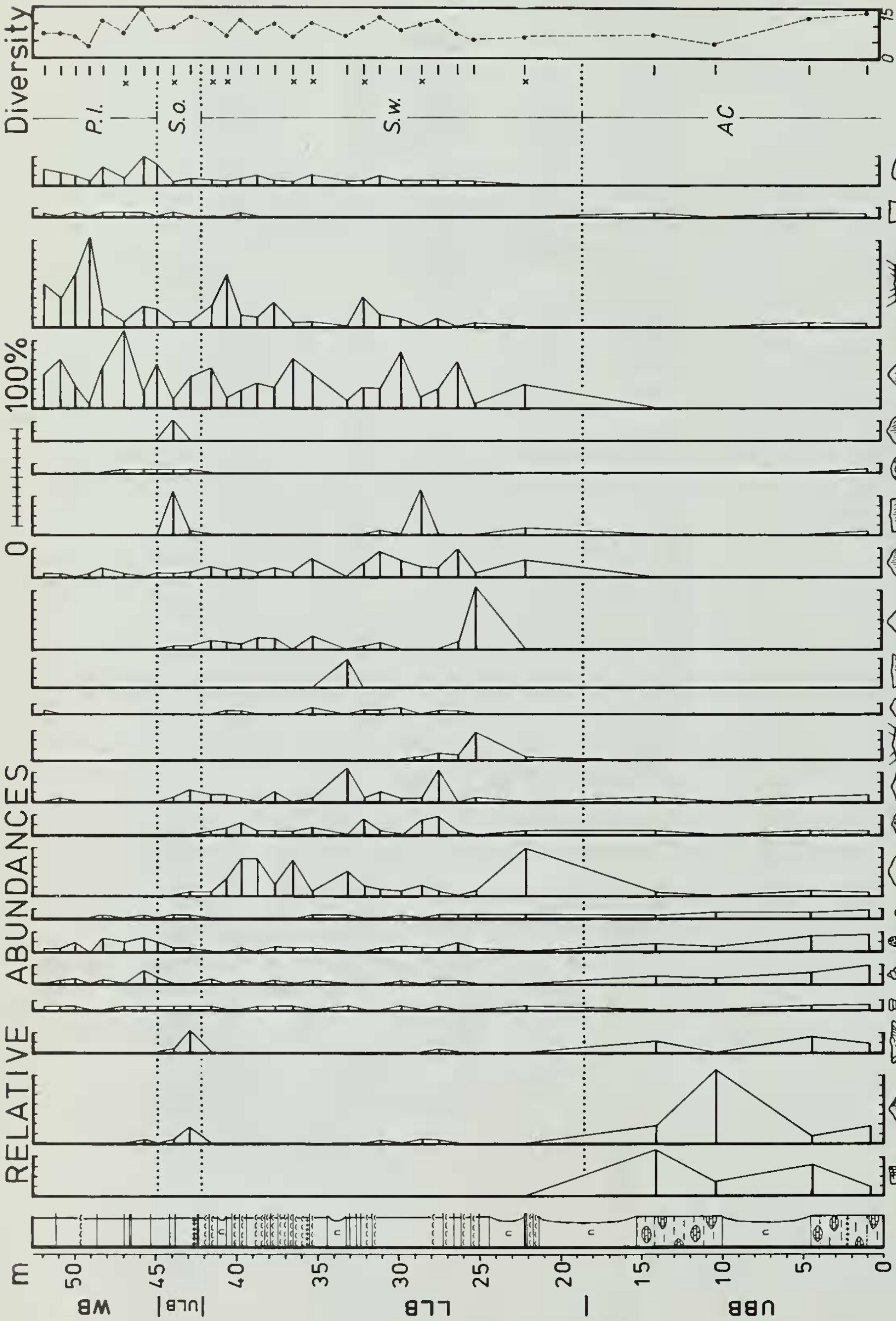


Fig. 18 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw) and *Atrypa reticularis* – coral Association (AC) in section 4A, near Ledbury. Symbols are explained in Figs 14 and 15. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. For more detailed sampling between 35–36 m within this section, see Figs 10 and 11.

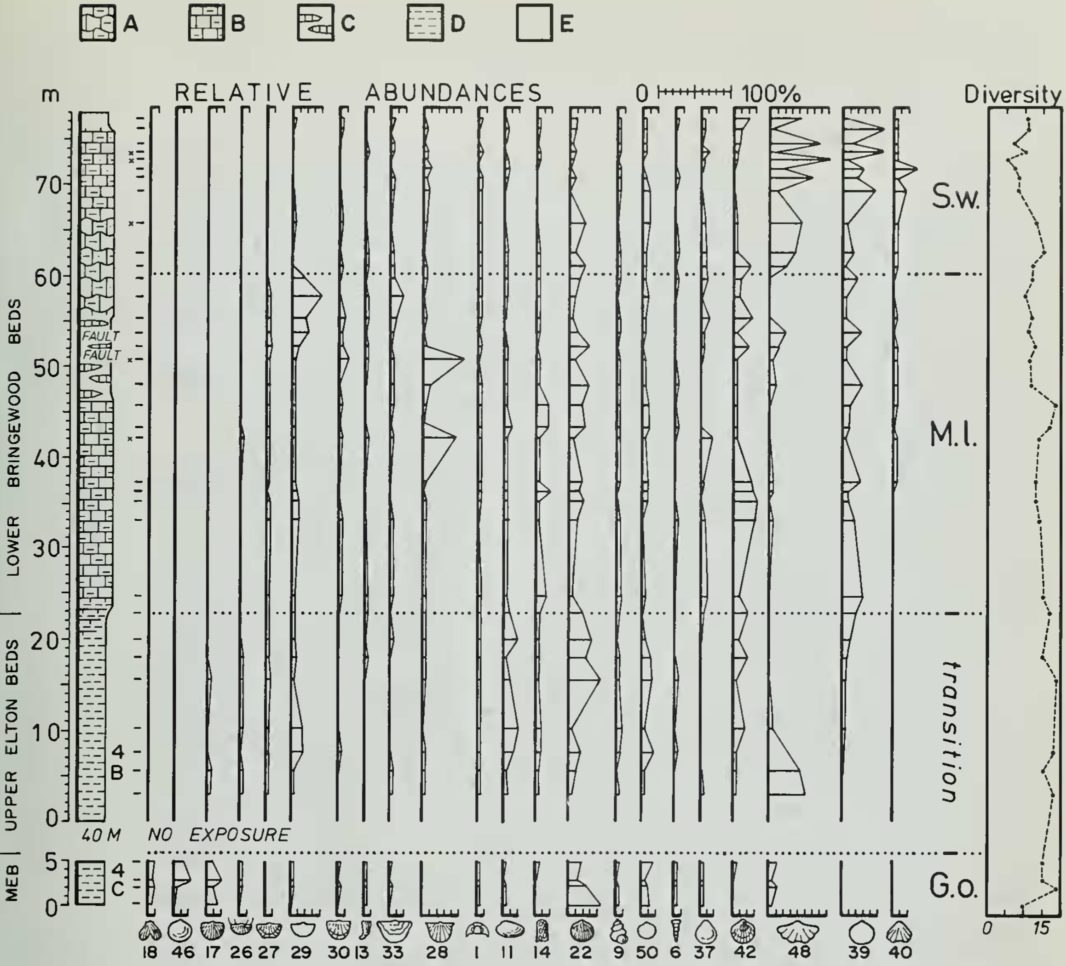


Fig. 19 Faunal profile of the *Sphaerirhynchia wilsoni* Association (Sw), *Mesopholidostrophia laevigata* Association (Ml), transition fauna and *Glassia obovata* Association (Go) in sections 4B and 4C, Ledbury. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. A – massive calcisiltite and silty limestone; B – bedded calcisiltite and silty limestone with shell layers; C – thinly interbedded calcisiltite and limestone; D – mudstone facies; E – bioturbated siltstone. Faunal symbols are explained in Fig. 15.

Small brachiopods with strongly incurved beaks and a probable unattached reclining mode of life are the most abundant life habit group within the *G. obovata* Association. Examples include *Glassia*, *Parastrophinella*, *Plagiorhyncha* and ?*Protozeuga*. *Isorthis* is the most common pedunculate form, but several other taxa with unrestricted pedicle openings, including *Skenidioides*, *Resserella*, *Dalejina*, *Dicoelosia* and *Howellella* are present. The only common strophomenides of the association, *Protochonetes minimus* and *Ludfordina pixis*, did not have a completely free mode of life, but show adaptation for stabilization by spines and a pedicle respectively. Fifty per cent of brachiopod species in the association are more common members of other Ludlow communities, and may be considered at the extremes of their tolerance ranges in the mudstone facies and laminated shale facies.

Bivalves

Twenty-two species of bivalves have been identified from the *G. obovata* Association. Five of

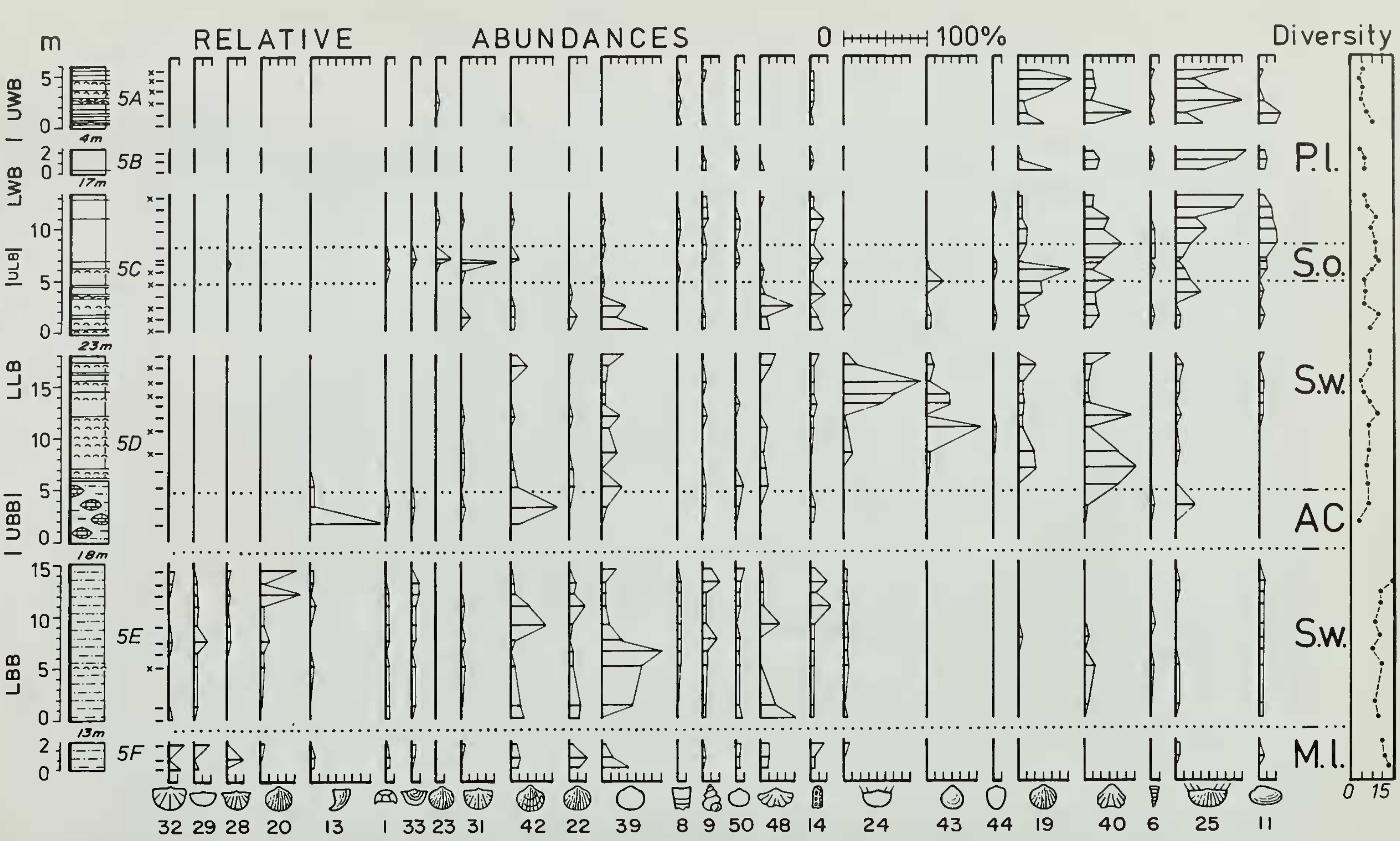


Fig. 20 Faunal profile of the *Protochonetes ludoviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw), *Atrypa reticularis* – coral Association (AC), and *Mesopholidostrophia laevigata* Association (Ml) in the Perton area. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. Other symbols are explained in Figs 14 and 15.

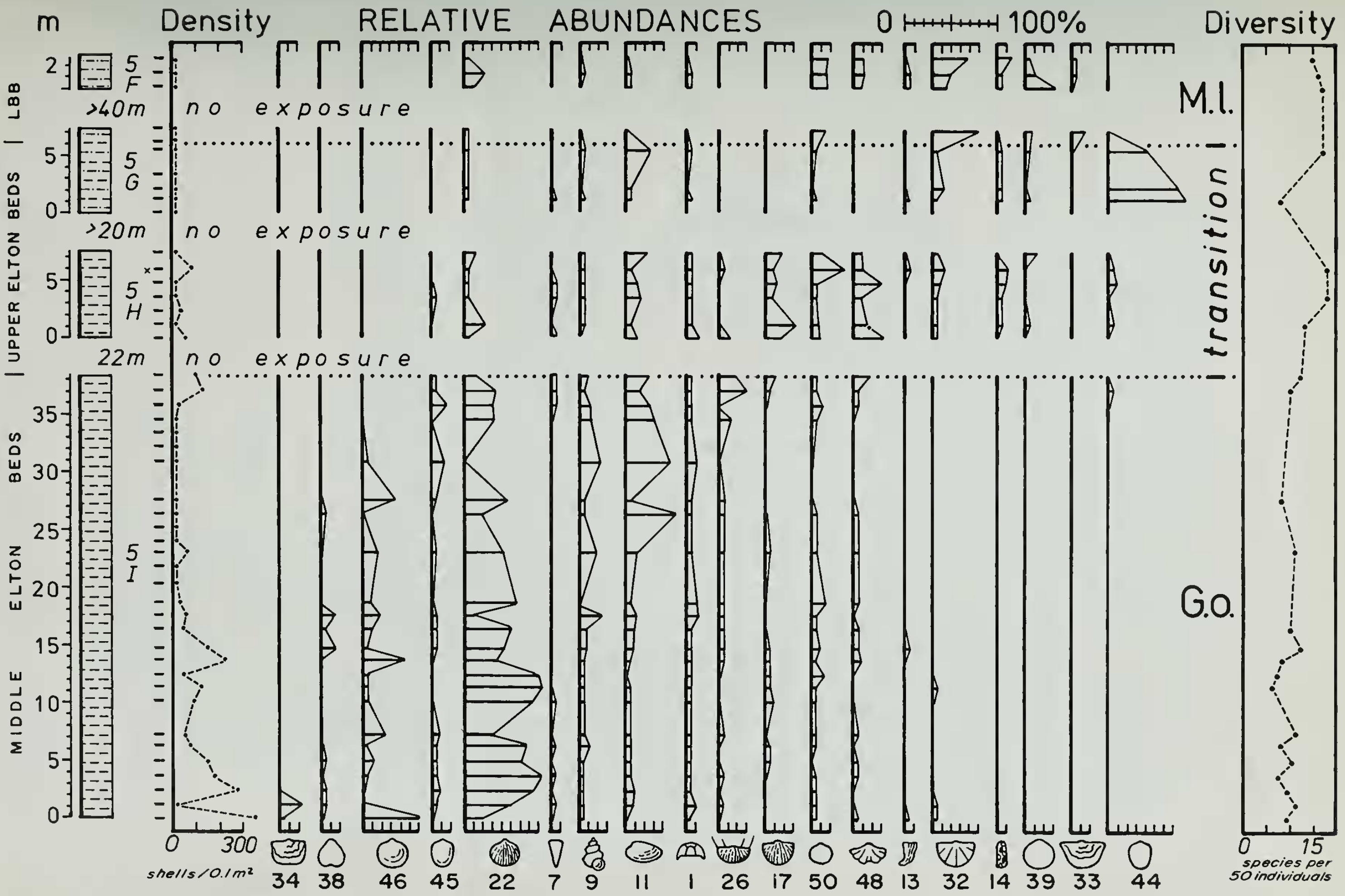


Fig. 21 Faunal profile of the *Mesopholidostrophia laevigata* Association (Ml), transition fauna, and *Glassia obovata* Association (Go) in the Perton area. Four bentonite beds occur in the lower 3 m of section 5I. See Figs 14 and 15 for explanation of symbols.

these species are members of the Praecardiacea, and are mainly restricted to the laminated shale facies. Like *Aegiria*, they have a distribution pattern which corresponds with that of graptolites, and are considered to have had an epiplanktic mode of life. These species are listed in Table 23 of the deposit data; see p. 179.

The free-burrowing nuculoids *Nuculites woolhopensis* and *Praenucula* sp. comprise about half of all bivalve individuals in the *G. obovata* Association. Most shells are below 1 cm in length. These species are commonly found together in samples, and occur throughout profiles of the association in both the mudstone facies and laminated shale facies. In a 10-m portion of bioturbated mudstone in section 51, *Nuculites* and *Praenucula* become the dominant taxa of the association, reaching combined relative abundances of 40–50% (Fig. 21). This interval corresponds to a decrease in density and relative abundance of brachiopods, and may relate to a decrease in substrate hardness, as discussed later. *Nuculites* and *Praenucula* are also among the most common members of the association in the laminated shale facies (Table 23, deposited). Two other species of small nuculoids, *Nuculites pseudodeltoideus* and *Praectenodonta ludensis*, occur rarely in the mudstone facies.

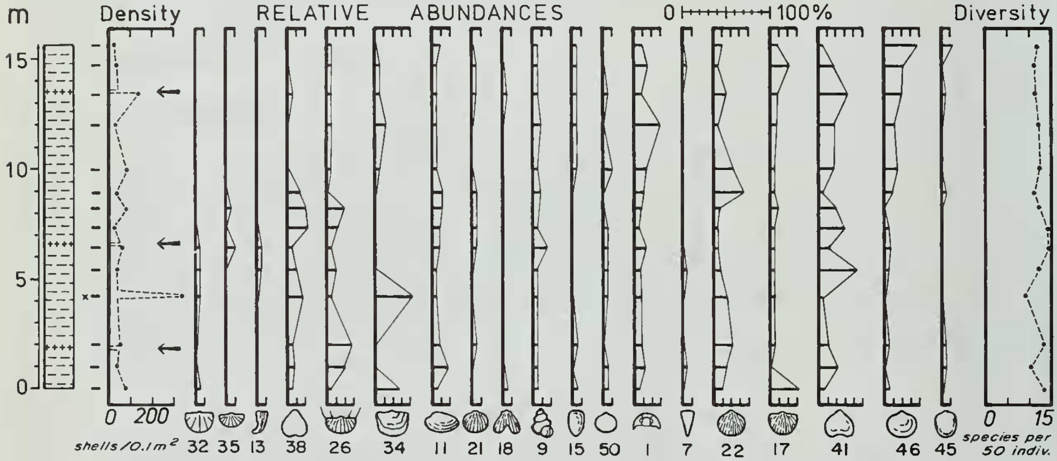


Fig. 22 Faunal profile of the *Glassia obovata* Association in section 1E, Middle Elton Beds, Upper Millichope. Arrows beside the density curve indicate faunal destructions by bentonites. Lithological and faunal symbols are explained in Figs 14 and 15.

Thirteen other bivalve species in the *G. obovata* Association show a very sporadic pattern of occurrence, and are seldom represented by more than one or two individuals per sample. This pattern can be seen in Table 17 (p. 269), and suggests small, widely-separated populations. Most of these species show adaptation for an endobyssate mode of life, but epibyssate and free-burrowing forms are also present.

Gastropods

Gastropods are continuously present throughout stratigraphic profiles of the association, but are seldom represented by more than a few individuals per sample. They are most conspicuous in the laminated shale facies and mudstone intervals dominated by nuculoids, where they reach 10% of the total fauna (Figs 21 and 23). The bellerophontaceans *Cymbularia* and *Sphenosphaera* and the high-spired *Loxonema* and *Sinuspira* predominate among the gastropod fauna, ranging from 5 to 20 mm in size. Ten other gastropod species are listed in Appendix 3.

Cephalopods

'*Orthoceras*' *dimidiatum* and '*O.*' *gregarium* are very common components of the *G. obovata* Association. They have maximum diameters less than 15 mm, no ornament except growth lines

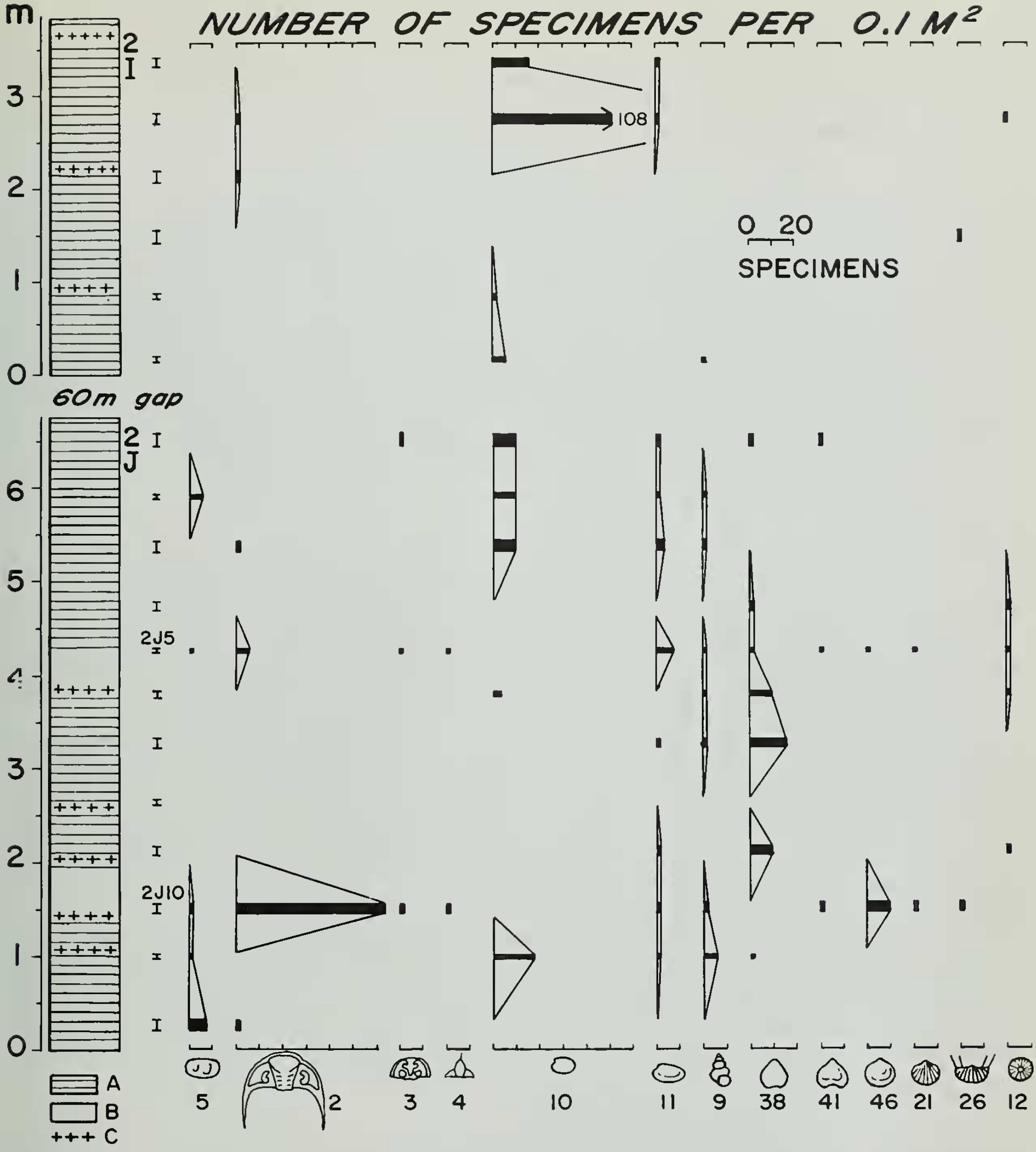


Fig. 23 Densities of benthic invertebrates of the *Glassia obovata* Association in sections 2I and 2J, Middle Elton Beds, Ludlow area. A – laminated shale; B – intensely bioturbated mudstone; C – bentonite. Faunal symbols are explained in Fig. 15.

and a simple orthoconic shell. These cephalopods reach maximum densities in laminated shales of basin and shelf edge areas, in association with graptolites. Like the graptolites, they show a decrease in density from Ludlow eastward across the shelf. This pattern indicates a pelagic mode of life, and lack of direct relation to bottom faunas.

Another group of cephalopods in the Elton Beds contrasts in their strong patterns of ornamentation, somewhat thicker shells, occasional departure from an orthoconic form and preferential association with benthic faunas rather than graptolites. These cephalopods are listed in

Table 15 (pp. 265–6) and include species of *Cyrtocycloceras*, '*Cyrtoceras*', *Dawsonoceras* and *Kionoceras*. They are rare or absent in the laminated shale facies, but occur sporadically throughout the mudstone facies with the *G. obovata* Association, generally in relative abundances of less than 1% of the total fauna. Their distribution suggests a nektobenthic mode of life and an ecological relation to bottom faunas, probably as predators.

Trilobites

Six species of trilobites have been recorded from the *G. obovata* Association, which appears to be their maximum diversity in Ludlow communities. *Dalmanites myops*, whose cranidia reach 4 cm in size, comprises 90% of this trilobite fauna. It is the most ubiquitous species of the association, and has been recorded in every sample from the mudstone facies. *Dalmanites* generally has a relative abundance of less than 5% of the total fauna, but becomes a dominant member of the association in the laminated shale facies. High densities of *Dalmanites* within the laminated shale facies correspond to discrete bioturbated intervals (Fig. 23), and this trilobite probably had a deposit-feeding mode of life. Other characteristic trilobites of the association include *Leonaspis coronata* and *Raphiophorus parvulus*, whose cranidia are less than 1 cm in size.

Minor groups

Hyolithes forbesi, a conical shell reaching 15 mm in length, is a minor but characteristic species of the *G. obovata* Association (Figs 21 and 22). Runnegar *et al.* (1975) demonstrated that hyolithids possessed a highly-folded gut, and suggested a deposit-feeding mode of life for the group. This is compatible with the consistent occurrence of *H. forbesi* in bioturbed mudstone.

Ostracods occur sporadically in samples of the association. In the mudstone facies, measured densities range from 0 to 24 valves per 0·1 m². Stratigraphic patterns of density in the laminated shale facies are shown in Fig. 23.

Crinoid ossicles are also sporadically present through the *G. obovata* Association, rarely occurring as articulated stem segments up to 2 cm in length. Observed columnals are 2 mm or less in diameter, and indicate very small individuals. Measured densities in the mudstone facies range from 7 to 20 columnals per 0·1 m², which is below the normal density for brachiopod valves. Crinoid individuals would thus have comprised far less than 1% of the fauna at any sampling station. In the laminated shale facies, ossicles of both calyx and stem occur on rare, small, circumscribed bedding surfaces, suggesting *in situ* decay of single individuals.

Bryozoa, solitary corals and tentaculitids occur very rarely in the *G. obovata* Association. The species of these groups are more abundant in other communities, and probably existed in the mudstone facies and laminated shale facies below the optimum of their environmental range. Extremely rare fossils known from the Elton Beds are large ceratiocarid crustaceans (Jones & Woodward 1888–89) and the echinoid *Myriastiches gigas* Sollas (Lister & Downie 1967).

Substrate and feeding relations in the association

Hancock *et al.* (1974) and Calef & Hancock (1974) considered great water depth and very low food supply as the most important environmental factors relating to the fauna of the Elton Beds and similar communities of the British Wenlock. The small size of brachiopod individuals in such communities was their chief evidence of low food supply. However, Lister (1970) recorded high densities of arcritarchs from the Elton Beds, indicating that the phytoplankton-derived food supply of the *G. obovata* Association may not have been extremely low.

The mudstone facies of the Elton Beds includes no sand and over 50% of clay, and is the most thoroughly bioturbated of Ludlow shelf sediments (Pl. 1, fig. 5). These relations indicate a soft, continuously reworked substrate, and suggest an alternative explanation for the small size of brachiopods in the *G. obovata* Association. Bokuniewicz *et al.* (1975 : 277) gave a formula for the depth to which an epifaunal animal would sink into soft sediment. A brachiopod maintaining a constant shape factor must decrease its radius and wet weight (that is, its overall size) to prevent increased sinking as it occupies bottoms of progressively lower hardness. Most brachiopods in the *G. obovata* Association could have elevated the commissure only a few mm above the bottom, and even a small amount of sinking into the substrate would have been critical. Thus small size would have been an important adaptation to a soft mud bottom.

Fürsich & Hurst (1974) stated that Spiriferida and Pentamerida maintained larger individuals relative to other brachiopods in 'deep water' environments of low food supply because they had more efficient lophophores. However, this feeding-related size factor also appears to be modified by substrate conditions. In the Elton Beds, which Fürsich & Hurst (1974) consider to represent a 'deep-water', nutrient-poor environment (the Ludlow *Dicoelosia* Community of their report), the dominant Spiriferida and Pentamerida are *Glassia obovata*, ? *Protozeuga* sp. and *Parastrophinella* sp. These species are less than 1 cm in mean size, and no larger than species of other brachiopod orders in the association.

The stratigraphic interval in section 5I where brachiopods decline in density and relative abundance and nuculoids become the community dominants may also be related to substrate conditions. This interval (Fig. 21) may represent conditions of extremely liquified sediment, suitable for nuculoids, but too soft to support brachiopods at the sediment surface. Rhoads & Young (1970) showed that modern nuculoid bivalves contribute to liquefaction of muddy substrates by their burrowing and feeding activities, and directly inhibit colonization by epifaunal suspension-feeders. Similar competitive exclusion and substrate conditioning may have occurred at the peak of nuculoid abundance in the *G. obovata* Association.

Occurrence of the association in the laminated shale facies

Stratigraphic profiles of the *G. obovata* Association in the laminated shale facies are shown in Fig. 23. Rare, isolated specimens of *Dalmanites*, *Nuculites*, *Praenucula*, *Cymbularia*, *Sphenosphaera* and *Parastrophinella* occur sporadically throughout most parts of the shale. Density of these forms is so low that they were probably not reproducing populations, but pelagically-recruited, non-reproducing individuals at their extreme limits of environmental tolerance. Indeterminate bivalves less than 1 mm in size are locally abundant in the shale (Fig. 23), and may represent early-shelled larvae of nuculoids or other benthic bivalves which died *en masse* shortly after settling on the laminated mud bottom. As discussed above, p. 193, low oxygen concentrations were probably the restrictive factor for bottom life in this environment.

The densest occurrences of *Dalmanites* and other members of the *G. obovata* Association in two intervals of bioturbated mudstone within the laminated shale facies (Fig. 23) probably indicate times of temporarily well-oxygenated conditions. Calef & Hancock (1974) made one collection from this type of fauna in the Middle Elton Beds near Ludlow. This sample was assigned to their '*Visbyella* Community', based on the supposed endemic occurrence of '*Visbyella trewerna*' and '*Clorinda dormitzeri*'. These taxa are synonomous with the *Resserella sabrinae nunfieldensis* and *Parastrophinella* sp. of this report. Both species occur throughout the Elton Beds of all shelf areas studied here, and they cannot be used to define a separate community in the shelf edge area around Ludlow. There is no evidence for a '*Visbyella* Community' in Ludlow sediments of the Welsh Borderland.

The statement by Calef & Hancock (1974) that their '*Visbyella* Community' represents 'the deepest limits of Silurian benthonic life' is also inapplicable to Ludlow faunas. The laminated shale facies of the Ludlow area is intercalated within a succession of shelf sediments (Fig. 3, p. 182), and cannot represent abyssal or very great depths. Sparse Silurian benthic faunas in laminated shales have also been related to extremely deep water by Boucot (1975) as 'benthic assemblage 6'. This interpretation ignores the importance of low oxygen levels in producing laminated shales with impoverished faunas, and is part of the undue emphasis which Silurian palaeoecologists have placed on water depth. Oxygen minima may operate over a wide depth range, as discussed by Shäfer (1972).

Transition from the *Glassia obovata* Association to the *Mesopholidostrophia laevigata* Association

Where the mudstone facies grades into the overlying bioturbated siltstone facies or calcisiltite facies, an extensive stratigraphic transition in fauna occurs between the *Glassia obovata* Association of the Elton Beds and the *Mesopholidostrophia laevigata* Association of the Lower Bringewood Beds. Discontinuous sections of this transition have been measured near Ledbury and Perton. The strata involved are assigned to the Upper Elton Beds on the basis of abundant *Pristiograptus tumescens* (Wood) in the Perton sections.

This ecological gradation is characterized by the disappearance of several characteristic fossils of the *G. obovata* Association. *Parastrophinella* sp. disappears relatively early, followed in order by *Glassia obovata*, *Leonaspis coronata*, ? *Protozeuga* sp., *Hyolithes forbesi* and *Praenucula* sp. Other forms, such as *Isorthis* and *Skenidioides*, decline in relative abundance. Bryozoa, stropheodontid brachiopods, *Sphaerirhynchia*, *Atrypa* and several other characteristic forms of the *M. laevigata* Association appear within the transitional interval in low but stratigraphically increasing abundances. Profiles of this transition are shown in Figs 19 and 21, and full faunal data are given in Table 15 of Appendix 3, pp. 263–6.

The transition between the *G. obovata* Association and *M. laevigata* Association occurs through a stratigraphic interval of about 30–50 m, and is completely gradual, reflecting a corresponding gradual change in sediment in which clay content decreases, bioturbation becomes less ubiquitous, swell lags of shells begin to appear and the amount of calcite cement increases. A change to a cleaner, less liquefied substrate under more agitated waters is indicated. The delimitation of a 'transition fauna' between the two associations in Figs 19 and 21 is a matter of convenience, and its boundaries are arbitrarily located at gaps in the stratigraphic exposure.

Mesopholidostrophia laevigata Association

The *M. laevigata* Association occurs in the calcisiltite facies and bioturbated siltstone facies of the Lower and Upper Bringewood Beds. It is the most diverse Ludlow shelf community, and is dominated by brachiopods and bryozoa. Swell lag assemblages of the *M. laevigata* Association are illustrated in Plate 4. Figs 16, 17, 19 and 20 show faunal profiles of the association, and complete faunal data are given in Appendix 3, Tables 15 and 18, pp. 270–1.

Brachiopods

Strophomenida are the most conspicuous brachiopods of the association, reaching sizes of 4 cm and comprising about one third of the total fauna. The 11 species present show a variety of adaptations for reclining upon soft sediment. These include stabilization by spines (*Protochonetes*), weighting of the posterior part of the ventral valve (*Mesopholidostrophia*), dorsal elevation of

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Plate 4

Mesopholidostrophia laevigata Association

Fig. 1. Sample 3A102, showing: a. *Mesopholidostrophia laevigata* (J. de C. Sowerby); b. *Leptostrophia filosa* (J. de C. Sowerby); c. encrusting bryozoan; d. *Sphaerirhynchia wilsoni* (J. Sowerby); e. *Atrypa reticularis* (Linnaeus); f. *Amphistrophia funiculata* (M'Coy). BB 73378. × 1·5.

Fig. 2. Sample 3A67, showing: c. encrusting bryozoan; g. *Dalejina hybrida* (J. de C. Sowerby). BB 73379. × 2.

Fig. 3. Sample 3A102, showing: b. *L. filosa*; c. encrusting bryozoan; e. *A. reticularis*; f. *A. funiculata*; h. '*Schuchertella*' sp.; i. *Isorthis clivosa* Walmsley. BB 73380. × 1·5.

Fig. 4. Sample 3A102, showing: a. *M. laevigata*; b. *L. filosa*; c. encrusting bryozoan; e. *A. reticularis*; i. *I. clivosa*; k. *Cypricardinia subplanulata* Reed; m. *Strophonella euglypha* (Hisinger); n. *Euomphalus* sp. BB 73380. × 1·5.

Fig. 5. Sample 3A67, showing: c. encrusting bryozoan; e. *A. reticularis*; g. *D. hybrida*; h. '*Schuchertella*' sp.; j. *Dalmanites myops* (König); l. *Howellella elegans* (Muir-Wood); o. unidentified conical shell; p. *Mytilarca siluriana* Reed. BB 73381. × 2.

All figures are of latex casts of 'swell lag' surfaces, coated with ammonium chloride, from the Lower Bringewood Beds at Woodbury Quarry. BB numbers refer to the brachiopod collections of the Department of Palaeontology, British Museum (Natural History).

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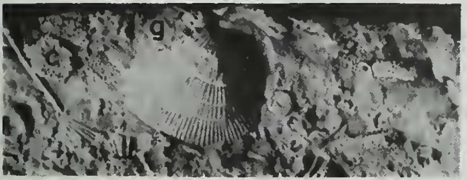

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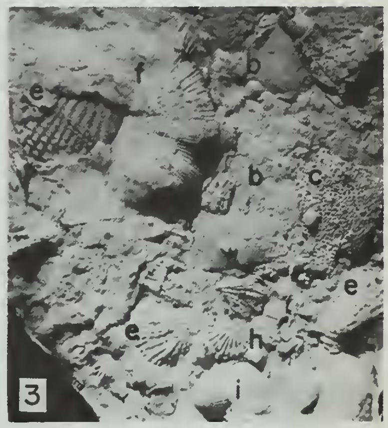

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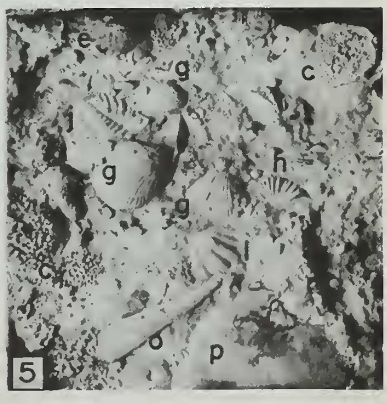


the commissure (*Strophonella*, *Amphistrophia*, *Leptaena*) and stabilization by a pedicle ('*Schuchertella*', *Lepidoleptaena*). Shell occurrence indicates that the freely reclining strophomenides must have been periodically disturbed by minor water agitation. Of 52 whole and disarticulated strophomenides in Woodbury Quarry, 63% were observed with convex sides upwards, 29% had convex sides downwards and 8% were orientated obliquely to bedding. In life orientation, individuals would have rested with the convex valve downwards and the commissure directed away from the substrate. The orientation data suggest that they were susceptible to frequent overturning to a hydrodynamically stable position. Abundance of strophomenides in the association indicates that this could not have had an adverse effect on their survival, and overturned individuals may have been able to right themselves by rapid snapping of the valves.

Shagamella ludloviensis is a strophomenide less than 5 mm in size which occurs throughout sections bearing the *M. laevigata* Association. It is usually present in low abundance, but shows very high densities locally. It also occurs abundantly in the laminated shale facies of the Upper Elton Beds near Ludlow, where it is associated with graptolites in the absence of a well-developed benthic fauna. *Shagamella ludloviensis* is considered, like *Aegiria*, to have had an epiplanktic mode of life. Its occurrences are given in Appendix 3, but it is not included in calculations or faunal profiles for the *M. laevigata* Association.

Twenty-one other brachiopod species in the association show adaptations for pedunculate or reclining modes of life. *Isorthis* and *Howellella* are the most common pedunculate forms, and *Gypidula*, *Sphaerirhynchia* and *Atrypa* are the most important of reclining brachiopods. Although no single brachiopod species dominates extensive stratigraphic intervals of the *M. laevigata* Association, any one of several species may predominate in single samples. These patterns of dominance show continuous fluctuations in stratigraphic sections (Fig. 17). In most species, temporary peaks of abundance are attained through gradual stratigraphic increases, followed by a decline and a stratigraphic interval of low abundance or absence. Complete cycles for a species occur over 5–10 m vertical intervals. These patterns of changing abundance are tested against a model of ecological succession in a following section.

Bryozoa

Bryozoa comprise 7% of the association, according to the method of counting, and occur with brachiopods on nearly every surface of rock (Plate 4). Owen (in Holland *et al.* 1963) listed 21 bryozoan species from the Lower Bringewood Beds of the Ludlow area, which indicates their high diversity in this community. Lamellose colonies encrust a high proportion of shell fragments, especially those of larger brachiopods. Colonies are less than 2 mm in height and in some cases extend around both surfaces of the shell fragment, indicating successful survival when the fragment was overturned. These forms are also present on the exteriors of whole brachiopods, and must have grown in part during the life of the host.

Other lamellose colonies grew partially or wholly on the sediment bottom. These forms have irregular bases corresponding to bottom configuration, and probably played a minor role in binding the sediment surface. They reach breadths of 3 cm, and vary from sheet-like to hemispherical in form. Globular colonies reaching 15 mm in diameter show growth on all surfaces, and could have survived if shifted in any orientation. Ramose branches extended from all colony forms, as indicated by broken basal attachments. Ramose colonies, reaching at least 4 cm in height, also grew directly upward from anchorages to shell fragments. Rare fragments of fenestrate bryozoa have also been found, but their relation to the substrate is unknown.

Molluscs

Bivalves comprise only 2% of individuals in the association, but are represented by at least 22 species. Patterns of occurrence can be obtained from Table 18. Most species occur in small numbers at widely separated stratigraphic intervals, and must have had very small, geographically restricted populations. Only *Cypricardinia subplanulata* and *Actinopteria sowerbyi* show a fairly consistent pattern of occurrence.

Nine species of gastropods also comprise about 2% of the association. *Bembexia lloydii*, *Leptozone striatissima* and *Oriostoma* sp. are characteristic forms, and reach maximum diameters of 2–3 cm. Rare cephalopods in the association are mostly ornamented forms like those interpreted as nektobenthic predators in the *G. obovata* Association.

Trilobites

Trilobites are very minor members of the *M. laevigata* Association, but occur continuously throughout stratigraphic profiles (Fig. 17). *Dalmanites myops* comprises about 40% of the trilobite fauna, and other species include encrinurids, calymenids and proetids. Five trilobite species have been found in this community during the present study, but additional forms in the Bringewood Beds have been listed by Holland *et al.* (1963) and Shergold & Shirley (1968).

Minor groups

Tentaculites, cornulites and conularids are represented by single species in the *M. laevigata* Association, and occur sporadically in samples in abundances of less than 1%. Many of the rare ceratiocarid crustaceans described by Jones & Woodward (1888–89) were probably also members of this community.

Solitary trochoid corals form 1·7% of individuals collected from the association. They show a fairly consistent stratigraphic occurrence, and reach diameters of 15 mm. These corals have been treated as a single taxon in diversity calculations, but have not been studied in section, and may represent more than one species. *Rhabdocyclus porpitoides* is a less common solitary coral. Syringoporid colonies are present on brachiopod shells and fragments, and colonies reaching 3 cm across also occur freely within the sediment.

Ostracods are locally common in the *M. laevigata* Association, and can be seen on all bedding surfaces illustrated in Plate 4. Shergold & Shirley (1968) listed several species occurring in the Lower Bringewood Beds of the Wenlock Edge area.

Crinoid columnals have an average density in bioturbated siltstone of about 4 per 0·1 m^2. Living individuals may have been more abundant than suggested by this figure, however, as crinoid columnals are abundant in shell beds of the bioturbated siltstone facies (Pl. 1, fig. 1), and have been preferentially sorted and concentrated. Columnals reach 9 mm in diameter, indicating the largest crinoid individuals in any of the Ludlow shelf communities. Columnals of this size are present in whole camerate individuals from the Wenlock Limestone of Dudley which reach heights of at least 20 cm.

Lawson (1973*a*) recorded the echinoid *Echinocystites pomum* Thomson and the ophiuroid ? *Urosoma hirudo* (Forbes) from the Lower Bringewood Beds of the Aymestrey area, which contain the *M. laevigata* Association.

Trophic structure of the *M. laevigata* Association

The *M. laevigata* Association contains the greatest trophic differentiation of the communities studied here, and emphasizes several problems pertinent to trophic analysis of Ludlow faunas. Suspension-feeding brachiopods are predominant, followed in abundance by suspension-feeding bryozoa and a number of other suspension-feeding groups, including bivalves, corals, crinoids, and possibly tentaculites and cornulites. Life habits and sizes of individuals in these groups indicate stratified levels of feeding above the sediment surface. Crinoids, possibly extending to 20 cm in height, were the highest feeders, followed by the tallest of ramose bryozoan colonies. These feeding levels were probably rather sparsely populated. Trochoid corals, various bryozoa and large brachiopods occupied a feeding level 1–2 cm above the bottom, and sheet-like bryozoa, small brachiopods and shallowly-buried bivalves fed very near the sediment surfaces. These were the most heavily utilized feeding levels in the community. Gastropods may have exploited a variety of feeding strategies, and cephalopods, present in very low abundance, have an acceptable occurrence pattern as predators.

On the basis of body fauna, deposit-feeding would appear to be limited to only a few per cent of community members, including nuculoid bivalves, possibly ostracods, and possibly many of the trilobites. However, the presence of *Chondrites* and extensive deformative bioturbation indicates a very active soft-bodied burrowing fauna. The majority of these burrowers were probably deposit feeders, and the *M. laevigata* Association can thus be considered as having had a mixed trophic structure with both epifauna and infauna abundant. Other Ludlow shelf communities show this same situation, although they probably had much less stratification of suspension feeding. *Chondrites* and deformative bioturbation indicate abundant deposit feeding in all sedimentary facies. The number of soft-bodied organisms or amount of deposit feeding relative to body fossils cannot be measured, however, and to this extent the trophic structure in Ludlow communities cannot be treated in a precise or quantitative manner.

Upper boundary of the *M. laevigata* Association

As indicated in Fig. 12, the *M. laevigata* Association is overlain by the *Sphaerirhynchia wilsoni* Association. In sections 3A and 4B, the stratigraphic boundary of these associations is marked by the disappearance or sharp drop in abundance and frequency of occurrence of species of '*Schuchertella*', *Strophonella*, *Amphistrophia*, *Mesopholidostrophia*, *Leptostrophia*, *Gypidula* and *Eospirifer* (Figs 17 and 19). At or slightly above the level of these disappearances and reductions, *Sphaerirhynchia wilsoni*, '*Camarotoechia*' *nucula* and *Howellella elegans* increase in abundance and become the dominant species of the *S. wilsoni* Association. These changes occupy a stratigraphic interval of about 5 m, and represent a permanent alteration in fauna. They occur within either the bioturbated siltstone facies or calcisiltite facies, and are not accompanied by any apparent changes in grain size, sediment composition, or sedimentary structures. The environmental cause of this transition is not clear, and it does not affect bryozoa, bivalves, gastropods, trilobites and minor phyla.

A clearly recognizable boundary between the *M. laevigata* Association and *S. wilsoni* Association is also seen in section 2D near Ludlow (Fig. 16). The same disappearances of brachiopod species noted above occur, and *Dayia navicula*, *Hyattidina canalis*, *Isorthis orbicularis* and '*Camarotoechia*' *nucula* either appear or sharply increase in abundance, to define the base of the *S. wilsoni* Association. Unlike the previous examples, changes in the non-brachiopod fauna also occur at this level, most notably a disappearance of corals and a marked reduction in abundance and diversity of bryozoa (Fig. 16). These changes occur through a stratigraphic interval of about 2 m within a minor development of the 'Aymestry Limestone' facies. Although they occur within a single rock type, they relate broadly to a sedimentary change, as most of the *M. laevigata* Association in this section, below the limestone, is contained within the bioturbated siltstone facies, while most of the *S. wilsoni* Association, above the limestone, occurs within the coquinoid siltstone facies. Change in substrate and increased sedimentation rates were probably responsible for the disappearance of corals, reductions in bryozoa, and alteration in the brachiopods.

Sphaerirhynchia wilsoni Association

The *S. wilsoni* Association is present in the bioturbated siltstone facies, calcisiltite facies, 'Aymestry Limestone' facies and coquinoid siltstone faces, which is the widest environmental range of any Ludlow shelf community in the study area. It has two separate stratigraphic occurrences, a lower phase in the Lower Bringewood Beds of the Perton, Ledbury, and Woodbury Quarry sections, and an upper phase in the Lower Leintwardine Beds of all areas studied (Fig. 12). Ecological distinctions between the two phases are discussed below, p. 230. Faunal profiles of the *S. wilsoni* Association are shown in Figs 10 and 16–20, and checklists of species are given in Appendix 3, Tables 15, 16 and 19.

Brachiopods

In the lower phase of the *S. wilsoni* Association, 27 species of brachiopods comprise 81 % of the total fauna. The dominant forms are *Sphaerirhynchia*, *Atrypa*, *Howellella*, '*Camarotoechia*', *Dalejina* and *Isorthis*. The separation of *Isorthis orbicularis* in the *S. wilsoni* Association from *Isorthis clivosa* in the *M. laevigata* Association is a matter of nomenclatural convenience. Although morphologically distinct at the extremes of their stratigraphic ranges, populations of these species grade continuously into one another through the Bringewood Beds. Stratigraphic patterns of abundance of most brachiopod species in the lower phase of the *S. wilsoni* Association are similar to those of brachiopods in the *M. laevigata* Association, and consist of gradual, stratigraphically peaking cycles of abundance. The lower phase is also characterized by the occurrence in low abundance of some of the previously dominant brachiopods of the *M. laevigata* Association.

In the upper phase of the association, within the Lower Leintwardine Beds, brachiopod diversity decreases to 19 total species. Abundance patterns of brachiopods become more unpredictable and reach greater extremes, and large fluctuations in composition of fauna occur over very short stratigraphic intervals, as shown in Figs 16, 17, 18 and 20. Any one of eight brachiopod species, including representatives of *Salopina*, *Isorthis*, *Protochonetes*, *Shaleria*, *Sphaerirhynchia*, '*Camarotoechia*', *Hyattidina* and *Howellella*, may comprise over 70% of the fauna in single samples. This pattern was investigated in small-scale detail in section 4A, as shown in Fig. 10. The results show that the extreme fluctuations in relative abundances occur over stratigraphic distances of only centimetres. Lateral sampling of bedding surfaces (Figs 7 and 9) shows that major changes in brachiopod fauna can occur over only a metre at the same stratigraphic horizon.

Profiles of brachiopod abundances in the upper phase, as constructed from samples at 1-m intervals, present only the general pattern of faunal variation in the Lower Leintwardine Beds. They suggest, but do not show in its entirety, the complexity of this variation, and sampling of the same section at different points would produce a quantitatively different pattern. Even a cm by cm sampling of the upper phase would be valid only for the particular stratigraphic line of transect, and would differ from a profile constructed a few metres laterally. Although part of these widely-fluctuating abundances of brachiopod species in the upper phase are taphonomic results of the occurrence of storm shell beds, the same extreme unpredictable changes in abundances are seen within disturbed neighbourhood assemblages.

Lawson (1975) also noted this extreme fluctuation of brachiopod species in the Lower Leintwardine Beds, and suggested that each band of shells dominated by a different single brachiopod species might be considered a separate community. This suggestion is to equate a community with a single-species population, and carried to its extreme, might recognize 8 or even 8! communities within the Lower Leintwardine Beds. The view taken here is that the upper phase of the *S. wilsoni* Association represents a single community dominated by several 'opportunistic' brachiopod species, each adapted to a strategy of temporary, intensive reproduction. This view follows the transect definition of a community, and not the definition of a community by some specified proportion of species. The basic ecologic unity of the upper phase of the *S. wilsoni* Association, according to the transect approach, can be easily seen in Figs 17 and 18.

Shagamella ludloviensis, which earlier was interpreted as an epiplanktic species, occurs throughout both phases of the *S. wilsoni* Association. In the upper phase, individuals reach 1 cm in size and show a convergence in shell form with *Protochonetes ludloviensis*, a definitely benthic form. These populations of large *Shagamella* in the Lower Leintwardine Beds show the same pattern of extreme fluctuations in abundance as those discussed above, and probably should be treated as benthic in mode of life. *Shagamella* is shown in faunal profiles for the *S. wilsoni* Association in Figs 18 and 20, but omitted from other diagrams. A complete record of its occurrence is given in Appendix 3.

Bryozoa

In the lower phase, bryozoa comprise 9% of the total fauna, and show the same diversity and morphological forms as those in the *M. laevigata* Association. Bryozoa decline to an average abundance of 3% of the fauna in the upper phase, and are represented mainly by ramose growth forms, with very few of the varied colonies described earlier. Owen (in Holland *et al.* 1963) listed seven bryozoan species from the Lower Leintwardine Beds of the Ludlow area, which indicates the lowered diversity of the group in the upper phase of the *S. wilsoni* Association.

Molluscs

Bivalves comprise 2% of the fauna in the lower phase, and the 17 species recorded are forms from the *M. laevigata* Association, with the same sporadic pattern of occurrence. Bivalves increase in abundance to 5% of the fauna in the upper phase, and 15 species have been recorded, a few different from those in the lower phase bivalve fauna. Bivalves reach local abundances of 20% of the fauna in the upper phase, and are dominated by '*Paracyclas*' *insueta*, *Nuculites antiqua*, *Pteronitella retroflexa* and *Sedgwickia amygdalina*. Individuals of these species reach larger sizes than most bivalves in preceding communities, and the latter two commonly attain lengths of 2–3 cm.

The gastropod fauna of the lower phase is also a continuation of that of the *M. laevigata* Association, and occurs continuously throughout the stratigraphic sections in low abundance (Figs 17 and 19). Six species of gastropods in the upper phase of the association have been recorded in a much more sporadic stratigraphic pattern of occurrence. Cephalopods comprise less than 1% of both lower and upper phases of the *S. wilsoni* Association.

Trilobites

Trilobites comprise 1·4% of individuals collected from the lower phase, and occur fairly continuously in stratigraphic sections. They comprise the same species as in the *M. laevigata* Association, and are dominated by *Dalmanites myops*. This fauna essentially disappears within the upper phase of the association, which contains only rare proetids and *Acastella spinosa*.

Minor groups

The same two species of tentaculite and cornulite occur sporadically throughout both lower and upper phases, comprising less than 1% of the total fauna. They are joined in the upper phase of the association by the tubiculous annelid *Serpulites longissimus*, which is also rare. The coral fauna of the *M. laevigata* Association is present in small numbers in the lower phase of the *S. wilsoni* Association, and disappears in the upper phase. Ostracods occur sporadically throughout both phases, but are not consistently present. They become extremely abundant at stratigraphically isolated intervals in the upper phase, numbering several hundred valves per 0·1 m^2. Kjellesvig-Waering (1961) reported rare eurypterids from stratigraphic horizons which bear the upper phase of the *S. wilsoni* Association. Crinoid columnals are locally abundant in transported shell beds of both phases, but number less than 10 per 0·1 m^2 in bioturbated sediment.

A rich fauna of complete crinoids, echinoids and asteroids is known from the Lower Leintwardine Beds of the Leintwardine area (Ramsbottom 1958, Hawkins & Hampton 1927, Spencer 1914–40). This fauna lived at the sites of channel bottoms (Whitaker 1962), and must have been preserved by very rapid sedimentation. Stratigraphically associated brachiopod faunas represent the upper phase of the *S. wilsoni* Association. Species of the Leintwardine echinoderm fauna may have been more widely distributed over shelf areas of the coquinoid siltstone facies, but if so have not been recognized because of complete disarticulation of their skeletal elements.

Ecological distinction of lower and upper phases

The coquinoid siltstone facies, containing the upper phase of the *S. wilsoni* Association, represents a higher energy environment with more rapid sedimentation than the bioturbated siltstone facies and calcisiltite facies, which contain the lower phase of the association. Most forms which decrease in abundance or disappear in the upper phase were probably adversely affected by increases in sedimentation rate. The disappearance of corals can be best explained in this manner, as well as the decline in diversity and abundance of bryozoa. The predominant ramose forms of bryozoa in the upper phase could have coped with sedimentation by upward growth, which would not have been possible for the sheet-like and globular colonies prevalent in the lower phase.

Upper phase brachiopods also show proportional shifts in life-habit groups with the incoming of the coquinoid siltstone facies. Many strophomenides and reclining brachiopods disappear, and rhynchonellides, with commissural deflections to minimize sediment intake, become the most consistently abundant forms in the upper phase. No brachiopod, however, could have withstood the periodic storm deposition of laminated silt. The 'opportunistic' population strategies of upper phase brachiopods, which involved high reproductive potentials and limited time spans at single sites, were probably as important an adaptation as shell form in the environment of the coquinoid siltstone facies. This is emphasized by local abundance in the coquinoid siltstone facies of *Hyattidina canalis*. This brachiopod possesses no ribbing or commissural deflections, and has an incurved beak which would have precluded or restricted the amount of pedicle attachment. According to shell form alone, it would seem best adapted to a quiet environment of low sedimentation rate (Fürsich & Hurst 1974). It is almost exclusively restricted to the coquinoid siltstone facies of the Leintwardine Beds, however, and was probably able to survive by an ability to maintain transient but dense populations.

Atrypa reticularis – coral Association

The lower and upper phases of the *S. wilsoni* Association are separated stratigraphically by the development of the *Atrypa reticularis* – coral Association, as shown in Fig. 12. The *A. reticularis* – coral Association occurs in the 'Aymestry Limestone' facies of the Upper Bringewood Beds near Perton, at Ledbury and at Woodbury Quarry, and is a low-diversity community dominated by its eponyms. It represents a distinct stratigraphic anomaly in the ecological development of the inner shelf faunas. Faunal profiles and checklists for the *A. reticularis* – coral Association are given in Figs 17, 18 and 20 and Table 15 of Appendix 3.

Brachiopods

Atrypa reticularis is the only common brachiopod of the association, and comprises 45% of the sampled fauna. Its size range, generally from 15 to 30 mm, is the same as that in other communities. *Atrypa* fluctuates in abundance within the association, ranging from less than 5% to over 70% of individuals in single samples. Other brachiopods in the association are species which are more common in the lower and upper phases of the *S. wilsoni* Association. Although many brachiopod species of the *S. wilsoni* Association range through the *A. reticularis* – coral Association, their frequency of occurrence and abundance become very restricted in this interval, as can be seen in Fig. 17.

Corals

The coral fauna of the association consists almost wholly of the solitary trochoid forms, found also in the Lower Bringewood Beds, ranging from 15 to 20 mm in diameter. They comprise 16% of individuals sampled, but fluctuate widely in abundance through sections, reaching 70% of the fauna in local, disturbed neighbourhood assemblages. Trochoid corals were entered as a single 'species' in the diversity calculations, sections for taxonomic study not having been prepared. Although they would appear to be rare in the Woodbury Quarry profile of the association (Fig. 17), an abundant occurrence was observed outside the sampling intervals.

A single *in situ* favositid colony, 30 cm in breadth, was observed within the 'Aymestry Limestone' facies of the Upper Bringewood Beds on a face of Perton Quarry.

Minor groups

Bryozoa comprise 15% of the association, and consist of the same colony forms as described for the *M. laevigata* Association. Hemispherical colonies of *Monotrypa*, reaching 3 cm in diameter, are one of the most common bryozoans. Crinoid ossicles are locally common, and portions of stems reaching 5 cm in length occur. The gastropod *Oriostoma*, comprising about 4% of individuals, is another common member of the association. Small calcareous algae are present in thin sections of samples.

Other groups in the association comprise well below 1 % of the fauna, and consist of species more commonly found in the *S. wilsoni* Association. These groups include bivalves, cephalopods, tentaculites and trilobites, and are listed in Appendix 3.

Anomalous nature of the association

The appearance of the *A. reticularis* – coral Association in shelf sections correlates with the development of the low-energy 'Aymestry Limestone' facies, and is marked by a great decline in density of fossils. In the Upper Bringewood Beds at Perton Quarry, the *A. reticularis* – coral Association occurs with an average density of about 20 shells per m^2. This is far below average densities for disturbed neighbourhood assemblages of the underlying lower phase of the *S. wilsoni* Association (380 shells/m^2) and overlying upper phase of the *S. wilsoni* Association (660 shells/m^2). The drop in shell density cannot be explained by increase in sedimentation rate, as it occurs within a fine-grained limestone showing no evidence of current deposition. Diagenetic factors can also be excluded because of good preservation of fossils and representation of many phyla. The low shell density in the *A. reticularis* – coral Association indicates a substantial drop in biotic productivity relative to stratigraphically adjacent phases of the *S. wilsoni* Association.

This drop in productivity is not accompanied by the appearance of any species new to the depositional area. Most forms from the preceding community disappear or become reduced in numbers, and a few increase in relative abundance, but not in overall density, to become the dominants of the *A. reticularis* – coral Association. The density and species changes, which mark the upper and lower boundaries of the association, are gradual and occupy stratigraphic intervals of 2–5 cm. These relations can be seen in Fig. 17.

The *A. reticularis* – coral Association does not represent a 'new 'community, but rather a restricted assemblage of forms from the lower phase of the *S. wilsoni* Association. It is a stratigraphic interruption in what would otherwise be a continuous ecological transition between the lower and upper phases of the *S. wilsoni* Association. This reflects the sedimentary interruption of the succession of terrigenous facies by the Upper Bringewood carbonates, which was discussed in the sedimentology section. The *A. reticularis* – coral Association is related in part to this change from a silty to a lime mud substrate.

The appearance and taxonomic restriction of the association is also related to the formation of a barrier system at the shelf edge, as detailed earlier. Shelf-edge barriers offer an explanation for the quiet-water features of the inner shelf 'Aymestry Limestone' facies, and probably produced very restricted water circulation, with lessened influences of basin and oceanic waters. This would not have affected salinity, as indicated by the phyla present in the inner shelf area, but could have altered conditions of phytoplankton abundance and nutrients available to benthic organisms.

Plate 5

Sphaerirhynchia wilsoni Association

Fig. 1. Sample RW4 (section 1C), showing: b. *Isorthis orbicularis* (J. de C. Sowerby); c. *Protochonetes ludloviensis* Muir-Wood; d. '*Camarotoechia*' *nucula* (J. de C. Sowerby); e. *Salopina lunata* (J. de C. Sowerby); g. *Sphaerirhynchia wilsoni* (J. Sowerby). BB 73382. × 1·5. Lower Leintwardine Beds near Millichope Park.

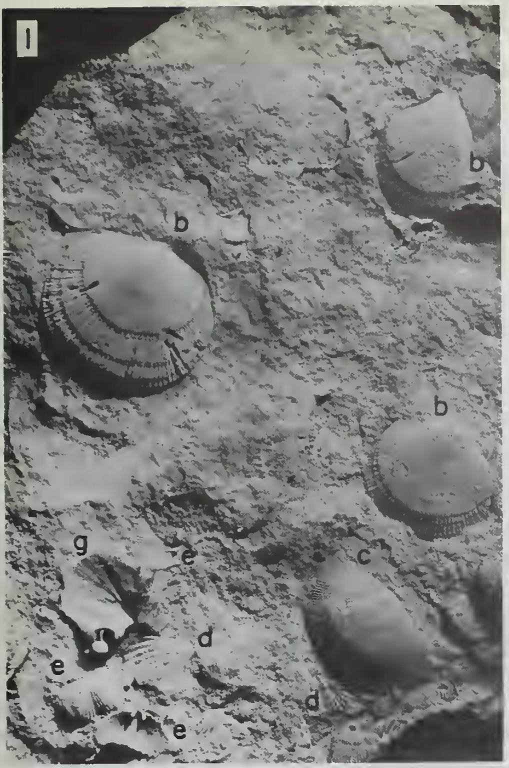
Protochonetes ludloviensis Association

Fig. 2. Sample 2B2, showing: a. *Nuculites antiqua* (J. de C. Sowerby); c. *P. ludloviensis*; d. '*C.*' *nucula*; e. *S. lunata*. BB 73383. × 1·5. Upper Whitcliffe Beds, Ludlow.

Fig. 3. Sample 4A3, showing: c. *P. ludloviensis*; d. '*C. nucula*; f. ramose bryozoan fragment. BB 73384. × 1·5. Whitcliffe Beds, Frith Wood, near Ledbury.

Fig. 4. Sample 2B2, showing: c. *P. ludloviensis*; e. *S. lunata*. BB 73385. × 1·5. Upper Whitcliffe Beds, Ludlow.

All figures are of latex casts coated with ammonium chloride. BB numbers refer to the brachiopod collections of the Department of Palaeontology, British Museum (Natural History).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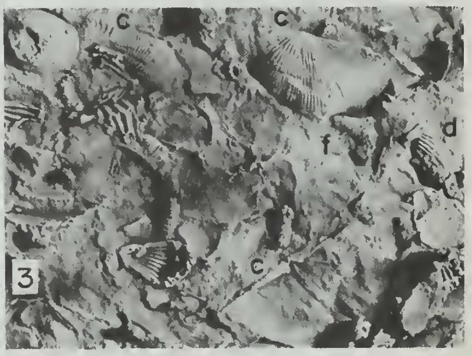
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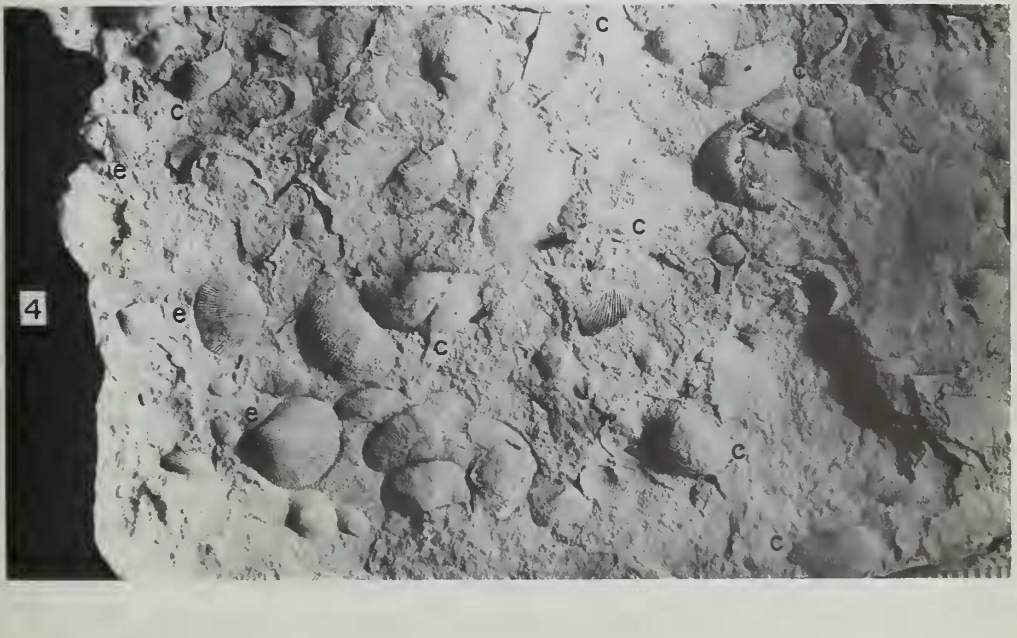
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Shaleria ornatella Association

The *S. ornatella* Association is the fauna which defines the Upper Leintwardine Beds in shelf areas, and it is confined to a restricted vertical interval of the coquinoid siltstone facies. This community occupies a consistent stratigraphic position between the upper phase of the *Sphaerirhynchia wilsoni* Association and the *Protochonetes ludloviensis* Association as shown in Fig. 12. It interrupts what would otherwise be a continuous gradation between these two communities, and is another ecological anomaly in shelf sections. Faunal profiles of the *S. ornatella* Association are shown in Figs 16–18 and 20, and counts for each species are given in Appendix 3, Tables 16 and 19.

Brachiopods

Shaleria ornatella is a free-lying strophomenide which occurs in low abundance throughout the *M. laevigata* Association, is rare in most parts of the *S. wilsoni* Association and returns in great abundance across the Welsh Borderland in the Upper Leintwardine Beds. *Leptaena depressa* and *Lepidoleptaena* sp. are other common Upper Leintwardine strophomenides which are also found throughout the *M. laevigata* Association, returning to shelf sections after an interval of rarity in the Lower Leintwardine Beds. These two species are adapted to partial burial in soft sediment, with a long trail elevating the commissure above the substrate. They are externally homeomorphic, and *Lepidoleptaena* is distinguished by the presence of a small pedicle foramen.

Isorthis clivosa is another common brachiopod of the *S. ornatella* Association. Ludlow *Isorthis* in the Welsh Borderland shows a continuous, environmentally-correlated morphological change from *I. clivosa* in the Elton Beds (*G. obovata* Association) to *I. orbicularis* in the Lower Leintwardine Beds (*S. wilsoni* Association). This change is a statistical phenomenon seen in entire populations, and involves an increase in size, relative decrease in shell depth and changes in articulation structures and muscle fields. The trend is abruptly terminated with the incoming of the *S. ornatella* Association, which correlates with a disappearance of *I. orbicularis* and the reappearance of *I. clivosa.* Upper Leintwardine populations of *I. clivosa* show greatest morphological resemblance to *clivosa* populations of the Lower Bringewood Beds (*M. laevigata* Association). These statements are based on a statistical study of several hundred specimens (Hurst & Watkins 1978).

Other common brachiopods in the *S. ornatella* Association are *Salopina lunata*, *Protochonetes ludloviensis*, *Atrypa reticularis* and '*Camarotoechia*' *nucula.* All of the species mentioned show extreme small-scale stratigraphic fluctuation in relative abundances. This indicates an 'opportunistic' pattern like that discussed for brachiopods in the upper phase of the *S. wilsoni* Association. Brachiopods comprise 87% of the total fauna collected from disturbed neighbourhood assemblages of the *S. ornatella* Association.

Bivalves

Bivalves comprise 7% of the association, and are the second most abundant faunal group. Free-burrowing, epibyssate and endobyssate species are present, but the latter comprise 86% of all individuals. The bivalve fauna of the *S. ornatella* Association is a continuation of that in the upper phase of the *S. wilsoni* Association, with the same dominant species. *Cypricardinia subplanulata* and *Mytilarca siluriana*, common bivalves of the *M. laevigata* Association, appear among the bivalve fauna of the *S. ornatella* Association after an interval of absence in the Lower Leintwardine Beds.

Trilobites

Trilobites are characteristic organisms of the *S. ornatella* Association, although they comprise only 1% of collected fauna. Their continuous presence throughout sections of the Upper Leintwardine Beds contrasts with their much rarer occurrence in the upper phase of the *S. wilsoni* Association (Lower Leintwardine Beds), as shown in Figs 17 and 18. *Calymene neointermedia*, *Encrinurus stubblefieldi* and proetids are the principal forms. This trilobite fauna resembles that of the Lower Bringewood Beds in general morphologic composition. Holland *et al.* (1963) and Shergold & Shirley (1968) have discussed the stratigraphic significance of the Upper Leintwardine trilobite fauna.

Minor groups

Minor groups recorded from the *S. ornatella* Association are ramose bryozoans, gastropods, cephalopods, tentaculites, cornulites, ostracods and crinoid ossicles. Details of all but the latter two groups are given in Appendix 3.

Anomalous nature of the association

The *Shaleria ornatella* Association occupies a stratigraphic interval of about 8 m at Ludlow and 1–5 m in shelf areas to the east. This thickness of strata is much less than that occupied by other communities in the coquinoid siltstone facies, and indicates a relatively brief duration of the association. In spite of its stratigraphic restriction, the *S. ornatella* Association is present in every Upper Ludlow section in the Welsh Borderland (Holland *et al.* 1963).

As shown in Fig. 12, the *Shaleria ornatella* Association occupies a stratigraphic position between the upper phase of the *S. wilsoni* Association (Lower Leintwardine Beds) and *P. ludloviensis* Association (Whitcliffe Beds). What would otherwise be a relatively simple ecological gradation between these two communities is interrupted by the stratigraphic appearance of the *S. ornatella* Association. Both lower and upper stratigraphic boundaries of the association are distinct enough to be located within intervals of 1 m (Figs 16–18). The *S. ornatella* Association marks the brief return of several characteristic forms from the bioturbated siltstone facies lower in the succession which are absent or rare in the intervening Lower Leintwardine Beds. The total faunal aspect of the *S. ornatella* Association is unlike that of surrounding communities in the coquinoid siltstone facies, and resembles the *M. laevigata* Association in the prominence of stropheodontids, leptaenids, *Isorthis clivosa*, *Atrypa reticularis* and trilobites.

The faunal relations of the *S. wilsoni* Association and *P. ludloviensis* Association, discussed later, indicate adjacent positions along an environmental gradient. Similar environmentally-controlled, superpositional relationships of *S. wilsoni*-type communities and less diverse *P. ludloviensis*-type communities have been described from the Wenlock of the Welsh Borderland (Calef & Hancock 1974) and the Pridoli of Nova Scotia (Watkins & Boucot 1975). Counterparts of the *Shaleria ornatella* Association are not seen in these community sequences. The stratigraphic position of the *S. ornatella* Association in the Ludlow of the Welsh Borderland does not represent an intrinsic position along an environmental gradient, and is interpreted as a single interruption of normal community development during progradation of proximal shelf deposits.

Environmental significance of the association

The environmental relations of the *S. ornatella* Association are best approached by considering those factors which do not appear to differentiate it from stratigraphically adjacent communities. These include the following.

1. Temperature, salinity, oxygen level. The broad faunal composition of the association clearly indicates that these factors could not have differed appreciably from other parts of the Ludlow sequence.
2. Bottom type. Grain size and composition are identical to sediment bearing different communities above and below.
3. Sedimentation conditions. An alternation of storm-deposited laminated beds and bioturbated siltstone is identical to other parts of the coquinoid siltstone facies bearing other communities.
4. Water depth. Following the sedimentary observations, it is very unlikely that depth of water over the Ludlow shelf changed significantly during Upper Leintwardine times.

5. Food supply. There is no evidence in acritarch abundance (Lister 1970) or size of benthic individuals to suggest any change in this factor.

After eliminating these factors, and considering that the *S. ornatella* Association is in part a reversion to the distal shelf fauna of the *M. laevigata* Association, a model involving larval dispersal may be proposed. Thorson (1950) observed that *Macoma* and *Syndosmya* communities of one part of the present inshore Danish waters are consistently recruited from larvae derived from a specific area tens of kilometres away, and not from larvae produced by local benthic populations. This is because of the prevailing current system, which disperses larvae from populations in one specific region to maintain bottom communities in another area.

From these observations, we may propose a temporary shelf-wide change in current system over the Welsh Borderland in Upper Leintwardine times. A change in current system could have carried larvae from distal shelf communities such as the *M. laevigata* Association to proximal shelf environments represented in the Upper Leintwardine Beds. These larvae, settling in a foreign environment, would produce an anomalous bottom community as long as these particular conditions of currents remained in effect.

There is no evidence for the location of the distal shelf environments which could have supplied larvae to areas where the *S. ornatella* Association is found. However, several faunal features of the *S. ornatella* Association conform with the model.

1. Brief, stratigraphically and ecologically disjunct occurrence of several species 'exotic' to the proximal shelf environment, such as *Isorthis clivosa* and *Mytilarca siluriana.*
2. Faunal dominance by leptaenids, *Shaleria* and *Atrypa*, which otherwise were of very low abundance and probably at the extremes of their tolerance limits in the coquinoid siltstone facies.
3. The addition of the exotic forms to the normal proximal shelf fauna rather than replacement (although substitution of *I. clivosa* for *I. orbicularis* is a notable exception).
4. The sudden appearance in the Upper Leintwardine Beds in both basin and shelf of species which are completely unknown in older strata (Lawson & Straw 1956). *Neobeyrichia lauensis* (Kiesow) and *Encrinurus stubblefieldi* are among these invaders.

The model is also supported by ecological aspects of graptolite distributions. In sections east of Ludlow, graptolites are extremely rare in the Bringewood Beds and Lower Leintwardine Beds and absent in the Whitcliffe Beds. They can be readily found with the *S. ornatella* Association in the Upper Leintwardine Beds, however – a monospecific assemblage of *Saetograptus leintwardinensis* (Lapworth). Surface currents carrying offshore larvae to proximal parts of the shelf would also carry plankton further inshore than usual. This would explain the very brief Upper Leintwardine incursion of graptolites over the shelf areas.

Synchrony and type section of the Upper Leintwardine Beds

If the model presented above is applicable, as suggested by several lines of evidence, then the *S. ornatella* Association must represent a synchronous ecological event. The synchrony of the Upper Leintwardine fauna has been accepted by Lawson & Straw (1956) and subsequent workers on the empirical basis of its short vertical range, wide geographic extent and inclusion of species new to the Welsh Basin.

In the type section of the Upper Leintwardine Beds, Holland *et al.* (1963 : 134) defined the base of this division as at the first occurrence of *Aegiria grayi*, *Calymene neointermedia* and *Encrinurus* sp. (now *E. stubblefieldi* Tripp). The type section has been sampled again here as section 2C, shown in Fig. 16. This sampling indicates that the base of the *S. ornatella* Association, as well as the incoming of common graptolites, occurs 2 m below the base of the Upper Leintwardine Beds as defined by Holland *et al.* (1963). The identity of the Upper Leintwardine Beds in shelf areas east of Ludlow has been established in this study and by Holland *et al.* (1963) on the basis of its whole faunal content, that is, the *Shaleria ornatella* Association. *Aegiria grayi* does not occur east of Ludlow (Holland & Lawson 1963), and the two trilobites are too rare to be consistently used for defining the base of the Upper Leintwardine Beds outside the type section.

The only practicable basis for identifying the base of the Upper Leintwardine Beds in the Welsh Borderland is the appearance of the whole *S. ornatella* Association. Correlations made on this basis do not correspond to the boundary of the Upper and Lower Leintwardine Beds as defined, but relate to a horizon 2 m lower in the type section. In practical terms of correlation, these upper 2 m of the type Lower Leintwardine Beds are of 'Upper Leintwardine' age.

Protochonetes ludloviensis Association

The *P. ludloviensis* Association is restricted to the coquinoid siltstone facies of the Whitcliffe Beds. It is a low-diversity community dominated by brachiopods and bivalves, and Pl. 5, figs 2–4 show representative assemblages of species. Faunal profiles of the association are shown in Figs 11, 16–18 and 20, and checklists of species are given in Appendix 3, Tables 16 and 20.

Brachiopods

Brachiopods comprise 82% of individuals collected from disturbed neighbourhood assemblages. *Protochonetes ludloviensis*, *Salopina lunata* and '*Camarotoechia*' *nucula* are the dominant species, and each may form as much as 80% of the fauna in single samples. *Howellella elegans* is also very abundant in the uppermost Whitcliffe Beds at Ludlow (Holland *et al.* 1963). Nine of the remaining 11 brachiopod species recorded from the association are extremely rare, and appear only sporadically in stratigraphic profiles. These, listed in Appendix 3, are survivors from the *S. ornatella* and *S. wilsoni* Associations, and were probably at the extreme of their environmental tolerance.

Protochonetes, *Salopina* and '*Camarotoechia*' show extreme small-scale fluctuations in abundance in stratigraphic sections (Figs 16–18 and 20). This corresponds to an unpredictable 'opportunistic' strategy of reproduction, as discussed for the upper phase of the *S. wilsoni* Association. As single assemblages, any brachiopod sample in the Whitcliffe Beds can be duplicated within the many faunal combinations shown in stratigraphic profiles of the upper phase of the *S. wilsoni* Association. The brachiopods of the *P. ludloviensis* Association are not new community elements, but simply a selection of the high diversity of species within the *S. wilsoni* Association.

Bivalves

Bivalves comprise 10% of all individuals collected from disturbed neighbourhood assemblages, but locally reach 30% of the fauna. Although they have not been observed to exceed brachiopods in number of specimens, they would often have exceeded brachiopods in biomass. Unlike brachiopods, bivalves of the association show no reduction in diversity relative to preceding communities, and 16 species have been recorded.

The endobyssate *Sedgwickia amygdalina* comprises 42% of total bivalve individuals. Other common species are *Goniophora cymbaeformis*, *Ptychopteria tenuistriata*, *Pteronitella retroflexa* and *Nuculites antiqua*. These species appear to show stratigraphic fluctuations in abundance similar to those of brachiopods (Tables 24 and 29), but sampling has not been extensive enough to document this fully.

Minor groups

Bryozoa consist almost wholly of ramose forms, and Owen (in Holland *et al.* 1963) listed three species from the Whitcliffe Beds at Ludlow, derived from the *P. ludloviensis* Association. Gastropods are present in low abundance, and represented mainly by *Bucanopsis expansus* and *Cyclonema corallii*. Cephalopods of probable nektobenthic habit are fairly continuously present (Fig. 17).

Ostracods have a sporadic and occasionally dense occurrence like those of the upper phase of the *S. wilsoni* Association. Rare trilobites are *Acastella spinosa* and *Homalonotus knightii*; *E. stubblefieldi* survives into the basal few metres of the association at Ludlow. Telson parts of the crustacean *Ceratiocaris* comprise 0·1% of the collected fauna, and whole individuals, exceeding 20 cm in length, were described by Jones & Woodward (1888–89). Kjellesvig-Waering (1961) discussed the eurypterid fauna at the stratigraphic horizon occupied by the *P. ludloviensis* Association. One eurypterid fragment, representing less than 0·1% of the collected fauna, was found in this study.

Crinoid columnals less than 2 mm in diameter occur in low density throughout bioturbated sediment, and occasionally are concentrated in transported shell layers. Ramsbottom (1958) recorded whole individuals of the crinoid *Cicerocrinus elegans* Sollas from the Whitcliffe at Ludlow, but gave no information to indicate whether they were from the Whitcliffe Beds or Leintwardine Beds. Allen & Tarlo (1963) recorded a low-diversity marine fish fauna in the Whitcliffe Beds.

Environmental relations of the association

In overall stratigraphic pattern, the *Protochonetes ludloviensis* Association is a restriction of previous faunas of the Leintwardine Beds rather than a 'new' community of replacing species appearing along an environmental gradient. This can be seen in the Woodbury Quarry section (Fig. 17). The *P. ludloviensis* Association is marked by significant reductions in diversity of brachiopods and bryozoa, but no reductions occur in bivalves. This suggests an increase in sedimentation rate, adversely affecting epifaunal lophophorate groups, but not affecting infauna. Sedimentary features in the coquinoid siltstone facies of the Whitcliffe Beds, described above (p. 189), indicate the highest relative sedimentation rates in the Ludlow shelf sequence. However, the *P. ludloviensis* Association appears in sections at Ludlow and Perton within an extensive interval of bioturbated sediment, before these features become common (Figs 16 and 20).

Relation of the association to Downtonian faunas

The upper stratigraphic boundary of the *P. ludloviensis* Association has been studied at Ludlow, where the final occurrence of the community is shown at the top of section 2A in Fig. 16. In this section, assemblages dominated by *Protochonetes*, *Salopina* and '*Camarotoechia*' occur up to the base of the Ludlow Bone Bed, with no reduction in species or general faunal change.

The Ludlow Bone Bed grades from a single bed of bone material, several cm thick at locality 7 of Holland *et al.* (1963), to two or more separate horizons of bone material 1 cm or less thick in section 2A of this report. This transition occurs over a lateral distance of about 100 m. The separate thinner bone layers are shown in Pl. 3, fig. 1; they have sharp, erosional bases and are overlain by parallel-laminated siltstone. The sedimentary features and lateral impersistence of the Ludlow Bone Bed are identical to shell beds interpreted earlier as rapid storm deposits. They do not indicate a slow in-place accumulation of the bone material.

The invertebrate fauna within the Ludlow Bone Bed and associated parallel-laminated siltstone is shown as the stratigraphically highest sample in Fig. 16. It is a typical transported assemblage of the *P. ludloviensis* Association, impoverished in infaunal bivalves. The *P. ludloviensis* Association completely disappears above the bone bed. This disappearance is correlated with other biological events. *Chondrites* and associated deformative bioturbation are present immediately below the Ludlow Bone Bed, but were not observed in strata above. Acritarchs dominate the microflora below the Ludlow Bone Bed, but are very rapidly replaced by spores of land plant type in beds above (Richardson & Lister 1969). These biological disappearances correspond to both an environmental and a temporal non-sequence. The sedimentary evidence indicates that the non-sequence is not represented within the bone bed, but at an erosional surface at its base.

The Downtonian fauna above the Ludlow Bone Bed consists of fish, eurypterids, molluscs, lingulids and ostracods. This brackish-water community occurs throughout the Welsh Borderland, and shows low species diversity and a very sporadic pattern of occurrence. The fish and eurypterid faunas are taxonomically distinct from those in the marine upper Ludlow deposits (Kjellesvig-Waering 1961; Allen & Tarlo 1963). Dominant invertebrates are *Modiolopsis complanata* (J. de C. Sowerby), *Platychisma helicites* (J. de C. Sowerby) and *Lingula cornea* (J. de C. Sowerby). Any of these species may form 100% of local assemblages.

The stratigraphic pattern of Ludlow communities

Discreteness and number of communities

Ludlow communities in the study area have been defined by distinctive overlaps in stratigraphic ranges and relative abundances of a complex of benthic invertebrates. The ranges and abundance changes occur along a sedimentary-environmental gradient preserved in stratigraphic sections, and for the most part reflect ecological phenomena rather than evolutionary events. Inspection of faunal profiles such as Figs 17 and 18 will show that species ranges form a finite number of distinctive overlaps, described as 'Associations', along the stratigraphic transect of depositional environments. Ludlow communities are intergrading, as discussed below, but the intergradation is not so complete that any arbitrary number of communities can be recognized. The presence of only a few 'natural' faunal divisions within the Ludlow of the Welsh Borderland is also implicit in the work of Holland *et al.* (1963) and Lawson (1975).

The relative stratigraphic discreteness of Ludlow shelf communities results from an interplay of two types of faunal patterns in measured sections. One pattern consists of temporal variation within an association, where sediments do not change, species composition remains relatively constant, but relative abundances of species fluctuate. This pattern represents faunal variation during the persistence of constant major environmental conditions. In the second type of faunal pattern, directional stratigraphic changes occur in the species present, with appearances, disappearances and shifts in relative abundances which do not return to any previous state. This type of pattern represents the stratigraphic gradation from one association to another, and is usually accompanied by a change in sedimentary facies. With the exception of the transition between the *G. obovata* and *M. laevigata* Associations, the gradations occupy thicknesses of strata much subordinate to those occupied by faunas showing the first type of pattern. It is this subordinate stratigraphic nature of faunal gradations that lends a discreteness and finite number to the associations defined in measured sections.

Boundaries between communities

The conclusions reached here on the discreteness of Ludlow communities may appear, at first sight, to be in conflict with those of Calef & Hancock (1974), who stated that Ludlow communities of the Welsh Borderland were continuously intergrading in faunal content. This statement was correct for their available data, which was derived from about 50 spot samples embracing most of the area shown in Fig. 1, p. 177. If only the average content of the associations recognized here is compared, they can indeed be considered as completely intergrading in properties such as diversity, abundance of certain forms, etc. Some of these general trends will be discussed later.

When considered by continuous stratigraphic profiles, however, boundaries between Ludlow communities emerge, in which major ecological changes in fauna can be located in a definite and often restricted interval of strata. These boundaries range from the 30 to 50 m gradational interval between the *G. obovata* Association and *M. laevigata* Association to the contacts of the *S. ornatella* Association, which can be located within a metre of strata or less. Variation in scale and other properties of boundaries reveal aspects of Ludlow communities which are not apparent in considering average content.

Most stratigraphic boundaries between Ludlow communities are marked by immigration of species into the depositional area. This may occur at the boundary in question, or some distance below it, with the actual boundary of communities showing an increase in relative abundance of the immigrants. Disappearances of species from the previous community also occur within or near the boundary interval, and changes in relative abundance may occur among forms which range between communities. The faunal changes at boundaries tend to occur among forms in a particular rank order, in the general fashion predicted by Johnson (1972). Some of these rank orders have been described above, pages 224 and 228.

Where the faunal changes occur through an extensive interval of strata, as between the *G. obovata* and *M. laevigata* Associations, we may postulate a very slow change in environment. This is corroborated by the gradual transition, in this interval, from the mudstone facies to overlying sediments. The boundary between the *M. laevigata* and *S. wilsoni* Associations, as seen near Ludlow (Fig. 16), also consists of an alteration in fauna, but occupies only about 2 m of strata. Here environmental changes appear to have occurred relatively quickly. The sharpest stratigraphic boundaries are those of the *S. ornatella* Association, which can be located within centimetres. It is significant, in this regard, that the *S. ornatella* Association appears to represent a hydrographical event, and not a change in bottom sedimentation.

A second type of boundary between Ludlow communities does not involve the arrival of immigrants, but is marked only by disappearances of forms and shifts in relative abundances. Such boundaries are seen at the bases of the *A. reticularis* – coral Association and *P. ludloviensis* Association, and result in a lowering of species diversity. Rollins & Donahue (1975) related this type of phenomenon to an increase in physiological stress upon organisms. It results in the formation of a 'relict' community from elements of a previously more diverse community.

The Ludlow community pattern as a product of environmental histories

Johnson (1972) has discussed how the discreteness of benthic communities varies according to the nature of environmental gradients. Sharp environmental breaks result in discrete benthic communities and intergrading environments result in extensive gradations between communities. In stratigraphic sections, the rate of environmental change is an important analogy to this situation. The apparent discreteness of most Ludlow communities can be related to long-term persistence of certain environmental conditions, alternating with more rapid intervals of environmental change.

One category of environmental change relates to the major stratigraphic patterns of terrigenous sedimentation, which were summarized in the sedimentology section, p. 192. Each of the three major terrigenous facies persists for several tens of metres before grading into a succeeding facies within a smaller stratigraphic thickness. This supports the concept that intervals of environmental change in the Welsh Borderland, producing community boundaries, were temporally subordinate to times of environmental constancy. The vertical sequence of communities found in the major terrigenous facies (in ascending order, the *G. obovata, M. laevigata, S. wilsoni* and *P. ludloviensis* Associations) represents the superposition of a normal lateral community sequence.

A second category of environmental change producing relatively discrete community boundaries in the Ludlow sections appears to be caused by temporary hydrographic anomalies in the depositional area. The *Atrypa reticularis* – coral Association is related to interruption of terrigenous depositional patterns by restricted circulation and back-barrier, carbonate muds. The *Shaleria ornatella* Association can be related to a change in current patterns affecting larval dispersal. Neither association relates to the terrigenous environmental gradient which affected other shelf communites. Instead, they represent unique temporal interruptions of this community sequence.

Both the number and level of discreteness of Ludlow communities in the study area are products of the history of the environments represented in stratigraphic sections. They appear to relate to the nature and rate of terrigenous progradation over the Welsh Borderland shelf, as well as to temporary hydrographic anomalies. The observed faunal patterns are almost certainly not a reflection of any intrinsic biological discreteness of Upper Silurian benthic communities. The same forms of life as those in the Ludlow shelf sections would probably show a different pattern of community number and discreteness in an area with a different environmental history.

Trends in species diversity

The stability-time hypothesis

Sanders (1968) proposed the stability-time hypothesis to explain diversity differences between two abstract types of marine communities.

1. 'Physically-controlled community' – Small numbers of eurytopic species, adapted primarily to the physical environment, are present. Physical conditions expose organisms to severe physiological stress, and fluctuate widely.
2. 'Biologically-accommodated community' – Large numbers of stenotopic species are

present, forming stable, complex associations developed through a history of biological interaction. Physical conditions are fairly uniform and constant through time.

Sanders (1968) stated that biologically-accommodated communities will grade into physically-controlled communities along an environmental gradient of increasing physiological stress. This gradient may be expressed across either space or time, and will involve an increase in species diversity with increasing environmental stress. Slobodkin & Sanders (1969) stated that unpredictable fluctuations in the physical environment will be a greater cause of physiological stress to organisms than predictable fluctuations.

Ludlow stratigraphic sections as an environmental stress gradient

The terrigenous sedimentary facies in Ludlow shelf sections represent a gradient of increasing environmental stress upon bottom faunas. Sedimentary conditions were most stable in the mudstone facies at the distal shelf end of the gradient. This is indicated by extreme uniformity of sediment, complete bioturbation and rarity of current-deposited beds. More variable sedimentation began in the succeeding bioturbated siltstone facies, with the introduction of minor erosion and sporadic distal deposition of laminated silt sheets. The proximal shelf coquinoid siltstone facies, at the top of Ludlow sections, represents the high-stress end of this environmental gradient. Decrease in bioturbation, frequent erosional surfaces, transported shell beds and frequent storm-deposited laminated silts in this facies show fluctuating patterns of deposition and very high local rates of sedimentation.

Faunal destructions caused by storm sedimentation may be considered a primary cause of biologically-directed stress in the Ludlow shelf environments. The frequency of storm-sedimentation events, as well as their probable intensity, increases stratigraphically from the mudstone facies to the coquinoid siltstone facies. Faunal destructions by bentonite deposition represents another type of biologically-directed stress. This type of event, however, was less prevalent than storm sedimentation, and distributed fairly equally across the shelf environments.

Diversity gradients in Ludlow communities

Indices of species diversity in communities of the major terrigenous facies are given in Table 13.

Table 13 Diversity indices for communities of the major Ludlow sedimentary facies. *The indices give the mean number of species at a sample of 50 individuals, based on the rarefaction method of Sanders (1968). Go – *G. obovata* Association; tran – transitional fauna between *G. obovata* and *M. laevigata* Associations; Ml – *M. laevigata* Association; lpSw – lower phase of *S. wilsoni* Association; upSw – upper phase of *S. wilsoni* Association; Pl – *P. ludloviensis* Association

stratigraphic unit	Elton Beds		Bringewood Beds		Leintwardine and Whitcliffe Beds	
facies	mudstone		bioturbated siltstone		coquinoid siltstone	
number of samples	(35)	(11)	(61)	(21)	(28)	(44)
association	Go	tran	Ml	lpSw	upSw	Pl
mean diversity per sample*	10·9	16·0	14·2	11·4	9·7	8·0

Average diversity values of the communities show a continuous decrease from the 'transition fauna' of the Upper Elton Beds to the *P. ludloviensis* Association of the Whitcliffe Beds. This decrease in diversity follows predictions of the stability-time hypothesis, and appears to be directly related to the increasing sedimentation-produced stress in the depositional environments. Stratigraphic plots of diversity by single sample show that this trend includes many small fluctuations on a metre-by-metre basis (Fig. 17). Although the overall decrease in diversity correlates with the pattern of sedimentary stress, species diversity at any particular point along the gradient appears to have been subject to second-order influences.

The *Glassia obovata* Association of the mudstone facies is an exception to the diversity trend. Although present in a distal shelf quiet-water environment with probably the slowest and most uniform sedimentation rate, it does not have the highest diversity of the Ludlow communities (Table 13). Softness of the muddy substrate, discussed on p. 222), may have limited the community to a particular diversity of specialized taxa, in spite of low-stress sedimentation conditions.

Biological accommodation

Although the broad diversity trend in Ludlow communities corresponds to predictions of the stability-time hypothesis regarding the effects of environmental stress, it is unlikely that diverse communities in the distal shelf environments of low sedimentation rate were truly biologically accommodated. If biological accommodation, resulting from a history of organism interactions, is a progressive process, we would expect to see diversity increases in communities with long persistence in a low-stress environment (Sanders & Hessler 1969). The *Mesopholidostrophia laevigata* Association is one of the most diverse Ludlow communities, and has been sampled through 60 m of constant bioturbated siltstone facies in Woodbury Quarry (Fig. 17). Although probably hundreds of thousands of years are represented by these strata, the association shows no increase in diversity. Instead, a general stability in diversity is seen, with values throughout the 60 m interval varying about a mean of 14–15 species per 50-individual sample size. Similar stable levels of diversity during temporal persistence of distal shelf conditions can be seen in Figs 5, 19 and 22. We will return to the topic of biological accommodation in the concluding discussion of Silurian benthic communities.

A stratigraphic consideration of opportunistic species

The numerical decline in species diversity within Ludlow communities in high stress sedimentary environments is directly related to the extreme dominance of samples by individuals of a single species. 'Opportunistic' species are those which are capable of rapid and temporary expansion in population size (MacArthur 1960). Many Ludlow species appear suddenly in great abundance and then wane or disappear over distances of centimetres or less in stratigraphic sections, particularly within the high-stress environment represented by the coquinoid siltstone facies. Hallam (1972 : figs 4–8) proposed a simple model which relates this type of stratigraphic phenomenon to MacArthur's concept of opportunism. According to Hallam's model, opportunistic species can be distinguished by great abundances of individuals which persist over only short stratigraphic distances. In contrast, Hallam (1972) proposed that 'equilibrium species' would be distinguished by a constant presence through stratigraphic sections without isolated peaks of extremely great abundance.

Hallam's model can be applied to Ludlow sections by the quantitative treatment of stratigraphic persistence of species and their relative abundance. We shall define Y as the maximum relative abundance a species reaches in any single sample. This indicates its maximum reproductive potential, relative to other species. X will be defined as the maximum number of continuous records of a species in samples taken at 1 m intervals along a stratigraphic section. This is a measure of its temporal persistence at a given depositional site. Note than low Y values for a species will normally bias its record toward low X values, as discussed in Appendix 2, p. 261.

Only certain of the Ludlow communities occupy stratigraphic intervals large enough to permit the use of this method, and only brachiopods are sufficiently numerous to lend themselves to the quantitative treatment. Plots of brachiopod species in the XY field, by community, are shown in Fig. 24. Species with plots falling in the upper left corner of the field, with high Y values (reproductive potential) and low X values (temporal constancy) can be considered as opportunistic. It is apparent that there is a gradation, rather than any natural breaks, in the positions into which various species fall when plotted within the field. An arbitrary line, drawn around the upper left corner of the XY field (Fig. 24), allows a consistent numerical definition of an 'opportunistic species', and permits relative comparisons to be made of the percentages of such species between different Ludlow communities.

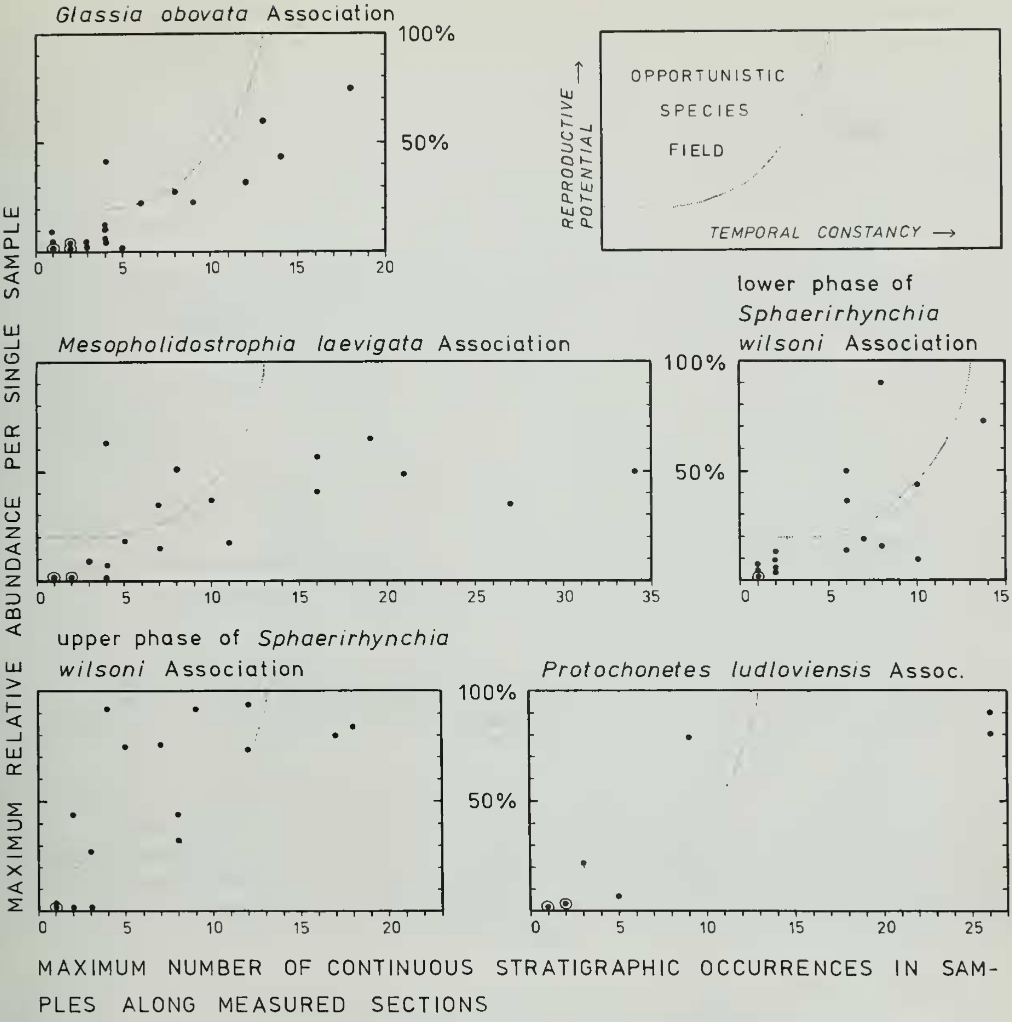

Fig. 24 Definition and comparison of opportunistic species in Ludlow communities. Dots represent values for single brachiopod species, and dots with circles represent several species. The 'opportunistic species field' is defined to include the major cluster of species in the upper phase of the *Sphaerirhynchia wilsoni* Association. This provides a method for making relative comparisons of opportunism between communities. Sources of bias in the plots and further discussion are given in the text.

Table 14 summarizes the *XY* plots in Fig. 24 according to the percentage of arbitrarily-defined opportunistic brachiopod species within Ludlow communities. The lowest percentage of opportunistic species is present in the *G. obovata* Association of the mudstone facies. Percentage of opportunists increase in communities of the stratigraphically higher bioturbated siltstone facies, and the highest percentage of opportunism occurs in the *S. wilsoni* Association of the coquinoid siltstone facies. Table 14 shows that, in general, the increase in environmental sedimentation-produced stress in Ludlow stratigraphic sections is accompanied by increased percentages within communities of brachiopod species with opportunistic patterns of occurrence.

Hallam (1972) also suggested that eurytopic species may change their population strategies over their environmental range. This is shown by several Ludlow brachiopods. *Isorthis*, for example, has plots as an 'equilibrium species' in communities of the bioturbated siltstone facies, but as an 'opportunistic species' in the *S. wilsoni* Association of the coquinoid siltstone facies.

The *P. ludloviensis* Association, at the most high-stress end of the stratigraphic-environmental gradient, is an apparent anomaly in the trend discussed above (Table 14). This is because most of its recorded brachiopod species are very rare survivors from previous communities. These species have plots in the lower left corner of the *XY* field (Fig. 24), and bias the calculation of opportunism within the association.

Table 14 Percentages of opportunistic brachiopod species in Ludlow communities, as determined by criteria in Fig. 24, p. 243. Go – *G. obovata* Association; Ml – *M. laevigata* Association; lpSw –lower phase of *S. wilsoni* Association; upSw – upper phase of *S. wilsoni* Association; Pl – *P. ludloviensis* Association

stratigraphic unit	Elton Beds	Bringewood Beds		Leintwardine and Whitcliffe Beds	
facies	mudstone	bioturbated siltstone		coquinoid siltstone	
association	Go	Ml	lpSw	upSw	Pl
number of brachiopod species	30	32	27	19	15
percent opportunistic species	3	9	11	53	13

The trends in opportunism within Ludlow communities correlate with observed features of the major terrigenous sedimentary facies, which suggests a direct relation to sedimentation-produced environmental stress. Susceptibility of populations to total destruction during storm-sedimentation events was probably a factor which favoured opportunistic reproductive strategies among Ludlow brachiopods, as discussed above, p. 231. Alternative explanations for the opportunistic patterns, not directly observable in the rock record, may also be involved. For example, fluctuating levels of food resources may contribute to dominance of marine communities by opportunistic species, and stable, and often lower, levels of resources may favour equilibrium species (Valentine 1971). Patterns of predation may also affect numerical fluctuations of particular species, as discussed later.

Faunal destructions in Ludlow communities

Bentonites and storm-deposited silts

As noted earlier, bentonites and storm-deposited sheets of laminated silt represent two types of biologically-destructive events preserved in Ludlow sections. Frequency of the later type of event shows a general correlation with decreased diversity of fauna and abundance of opportunistic species, as we have seen. In this section, we wish to test whether these events have any specific effect on the small-scale stratigraphic variation within particular communities.

Bentonites contain no burrows or body fossils, and extend laterally for great lengths along Ludlow outcrops. They were probably formed by rapid ashfalls, killing the benthic faunas on which they settled. Shells immediately below a bentonite are usually widely scattered and variably orientated, as elsewhere in bioturbated sediment. Storm-deposited laminated sheets of silt also rapidly buried and destroyed benthic faunas at particular sites. Concentration of epifaunal shells at the base of these sheets, burial of infaunal shells below them, and lack of escape trails indicate this total destruction. By analogy with modern processes, these destructive events were probably of very short duration, occurring over a day or less. Bentonites and storm-deposited silts are overlain by fossiliferous bioturbated sediment, indicating a return of normal, slow sedimentation following ashfalls or storms, and recolonization of the new sediment by benthos.

A model of recolonization

Ecological succession is a process by which a community at a particular place changes predictably in composition through time, either through change in physical environment, the effects of biotic activity of organisms, or both. Johnson (1972) proposed that succession is an integral part of marine benthic communities, and has developed a predictive model around this concept. Following theoretical considerations by Margalef (1968), Johnson's model states that a benthic community can exist in either an immature, early stage of succession, or later, mature stages of succession, which develop in an orderly, predictable fashion from the former state. Destructive physical disturbances of the environment will downgrade a community to its earliest successional state, following which it can gradually return to maturity through processes involving an increase in species diversity, increase in inert organic matter and biogenic structures, and decrease in fluctuations of population size. Stratigraphic sections of sediments with repeated environmental disturbances should contain communities showing repetitive successional events, each beginning with a downgrading following a disturbance.

Johnson (1972 : 155) considered the way succession would proceed when organisms recolonize a bottom following destructive events such as ashfall or storm-sedimentation.

> A newly deposited sediment is a relatively homogeneous habitat. As organic detritus accumulates at the sediment-water interface, the animals rework it into the underlying sediment. Through their feeding and burrowing activities, the sediment becomes increasingly heterogeneous on a small scale. The particle size, composition, and stability of the sediment may be altered . . . In addition, the activities of micro-organisms must profoundly affect the chemical environment. The accumulation of shells and burrows would further add to the heterogeneity of the infaunal environment . . . These modifications of the sediment must be accompanied by faunal changes. We would expect that the attractiveness of the substrate to settling larvae would change . . . In the beginning, species diversity would be low in the relatively homogeneous sediment. As the sediment becomes progressively more heterogeneous, providing more microhabitats, diversity should rise.

Comparison of the model with Ludlow faunal profiles

Fig. 25 shows a small-scale vertical profile of the *M. laevigata* Association which is interrupted by two bentonite beds. From this profile, we may note the following.

1. Density of shells per surface area of sediment immediately above the bentonites is in one case the same, and in one case higher than immediately below bentonites and in other parts of the section.
2. Species diversity immediately above both bentonites is not lower than in other parts of the section.
3. Species content immediately above a bentonite does not differ from that immediately below, either in the species present or the relative abundance of their individuals. The two bentonites do not divide the faunal profile into two repetitive faunal cycles.

The small-scale example shown in Fig. 25 is a detail of the larger faunal profile for the Woodbury Quarry section (Fig. 17). Again, in the larger section, there is no evidence of repetitive cyclical development of diversity and faunal patterns relating to bentonites. This same relation is seen in several other sections, shown in Figs 16, 21, 22 and 23. Storm-deposited beds of siltstone also appear to have no downgrading effect upon Ludlow communities. In Fig. 10, for example, note that sample 4A37, immediately above a storm-silt bed, does not show lower species diversity than samples 4A39, 4A40 and 4A42, which were taken from bioturbated sediment several centimetres above such storm-silts.

It is not possible to detect any downgrading or repetitive succession in Ludlow communities caused by bentonites or storm-deposited silts. The sedimentary record above such beds indicates an apparent immediate recolonization by the same species, often with the same quantitative proportions of individuals, as existed before the destructive event. However, some initial biotic conditioning of sediment, as discussed by Johnson (1972), must have preceded this recolonization. Rates of reworking by macrofaunal burrowers could produce substantial modifications of the sediment within days (Rhoads 1963), and chemical changes caused by micro-organisms may be as rapid. If a succession from micro-organisms to macro-burrowers to epifaunal assemblages can occur within days or weeks, it would probably be undetectable in a stratigraphic section. The key aspect of this problem is rate of shelf sedimentation. Apart from storm events, sedimentation rate on the Ludlow shelf was probably much slower than the time required for a sediment-conditioning type of succession. If such sediment-conditioning affected the order of arrival of shelled colonists, slow sedimentation rate would insure that virtually all successive arrivals were preserved in the same few millimetres of strata.

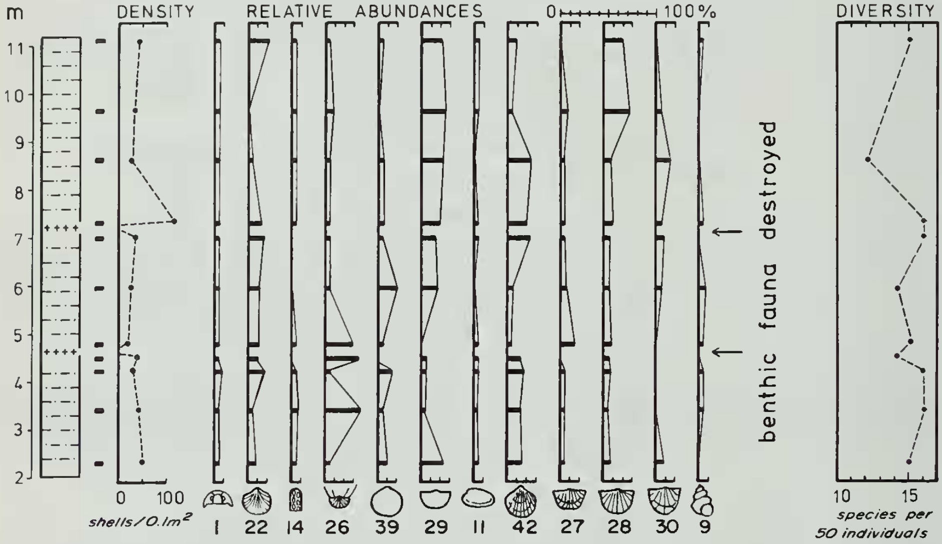

Fig. 25 Detail of the *Mesopholidostrophia laevigata* Association in section 3A, Lower Bringewood Beds, Woodbury Quarry. Note the lack of relation of faunal patterns and the diversity curve to the two intervals of faunal destruction. Metre readings locate this profile in the larger section shown in Fig. 17. Lithological and faunal symbols are explained in Figs 14 and 15.

Stratigraphic variation within communities

Variation within distal *versus* proximal shelf environments

As discussed in a previous section (p. 239), a basic identity is given to each of the Ludlow associations by a stratigraphic interval in which species content remains generally the same, and relative abundances of most species fluctuate back and forth. This pattern represents variation within a community during the relatively long-term persistence of certain major environmental conditions. In the proximal shelf, coquinoid siltstone facies, variations in relative abundances are extreme, and occur unpredictably in stratigraphic sections, literally centimetre by centimetre. This has been related to opportunistic strategies of reproduction in the dominant species within this environment. A contrasting pattern is seen in the mudstone facies and bioturbated siltstone facies, which represent distal shelf environments of lower physiologic stress. Here, many brachiopod species of the *G. obovata* and *M. laevigata* Associations show gradual stratigraphic cycles in abundance, in which the relative abundance of a species in any particular sample can generally be predicted from information on its abundance in samples above and below. These fluctuations occupy several metres of strata, and may relate to time spans of hundreds or thousands of years. They are not related to bentonites, as will be discussed later, and occur within very uniform bioturbated silt and clay.

Johnson's model of succession

Johnson (1972 : 152) has expressed this problem as follows.

> We do observe changes in species composition in modern communities without any noticeable change in the overall physical environment. Similarly, we commonly observe changes in continuous stratigraphic sequences that are not accompanied by any obvious change in lithology. Some of these may be the result of the vagaries of recruitment. More often such faunal changes probably are the result of the ecological interactions involved in succession.

Although Johnson's concept of succession has been shown to be inapplicable to the preserved faunal record relative to Ludlow bentonites and storm-silt beds, it must still be tested against those fluctuations which do occur in Ludlow communities. According to the model, successions seen in stratigraphic sections would involve faunal repetitions, each consisting of an ordered serial set of successional stages. Following some type of environmental disturbance, the community at a particular site would be downgraded to its earliest serial stage of succession. According to Johnson (1972) and Walker & Alberstadt (1975), this stage would be characterized by low species diversity, and dominated by a small number of those species of the community which are most eurytopic, or capable of existing outside the community's habitat. If the disturbing event does not persist, and the environment returns to some optimal condition, the model states that the community would undergo succession through progressively more mature stages, eventually reaching some sort of climax and equilibrium state. Walker & Alberstadt (1975 : fig. 1) have indicated some of the expected events in such a succession. For our purposes, the two most important are an increase in species diversity and an increased representation of 'characteristic species', that is, relatively stenotopic forms which are generally restricted to the particular community in question.

We will compare this model with the stratigraphic profile of the *M. laevigata* Association in Woodbury Quarry (Fig. 17), which shows many fluctuations in brachiopod species involving the regular increases and decreases in relative abundance of each species described earlier. The critical point is whether the stratigraphic fluctuations of each species relate to one another in the ordered, repetitive manner predicted by the model.

First, consider some 'characteristic species', restricted wholly or mainly to the *M. laevigata* Association: *E. radiatus* (taxon 49 in Fig. 17), '*Schuchertella*' sp. (taxon 36), *S. euglypha* (taxon 30), *A. funiculata* (taxon 27), *M. laevigata* (taxon 29) and *L. filosa* (taxon 28). All show cyclical patterns of abundance in the stratigraphic section. Next, consider those species which are present in the *M. laevigata* Association, but also commonly occur in other communities ('ubiquitous' and 'intergrading' species of Johnson 1972): *D. hybrida* (taxon 20 of Fig. 17), *A. reticularis* (taxon 42), *Isorthis* (taxon 22) and *S. wilsoni* (taxon 39).

If the stratigraphic variation within the *M. laevigata* Association conformed to the model of succession, we would see the following repeated pattern: 1. A stage with low species diversity and high abundance of taxa 20, 22, 39 and 42; 2. Gradual increase in species diversity accompanied by appearance of the 'characteristic' taxa listed above; 3. An interval of highest diversity consisting mainly of equitable abundances of the 'characteristic' taxa; 4. A downgrading of the community to the first stage and repetition of the succession.

No such pattern is apparent in the faunal profile in Fig. 17. The 'intergrading' and 'ubiquitous' species in the *M. laevigata* Association do not reach maximum abundances which, according to the model, would precede the appearance of the 'characteristic' species. The 'characteristic' forms are not restricted to stratigraphic intervals of highest species diversity of the community. In summary, neither the specific faunal sequence nor the repetitive aspects predicted by the model are apparent in the *M. laevigata* Association of Woodbury Quarry (Fig. 17). A similar situation can be seen in other faunal profiles in Figs 19–22. The stratigraphic variations within the *M. laevigata* and *G. obovata* Associations are probably not the result of repetitive ecological succession.

A model of temporal variation in larval recruitment

In the quotation presented earlier, Johnson (1972) noted a second explanation for fluctuations in community composition within a stratigraphic section under the phrase 'vagaries of recruitment'.

Studies of the recruitment of modern shallow communities in Danish waters show less randomness in this process than might be supposed, and provide a basis for constructing a model to test in stratigraphic sections.

Coe (1957), Johnson (1970) and Parker (1975) showed that temporal variations occur in shallow marine communities over periods of several years with no observed correlative change in the environment. The most extensive series of observations documenting this phenomenon are those of Blegvad (1925, 1928), who monitored the composition of shallow communities in the Danish Limfjord between 1910 and 1927. Blegvad's data show that although the species composition at particular sites remained relatively constant over this period, the densities of individuals of each species (and thus, their relative abundance) varied considerably. During certain successive years, densities of particular species remained low, and in other successive years, densities increased to some highest value before falling. Graphic presentation of these data by Blegvad (1925, 1928) shows no evidence of repetitive ecological succession relating to the fluctuations of species. Blegvad (1928) found that fish predation affected the temporal pattern of the fluctuations, but noted no other influences of biotic interaction or benthic environmental change.

The number of planktic larvae in the water column was the major factor associated with the fluctuations in abundance of each species. Blegvad (1928) observed that times of high density of benthic individuals of a particular species correlated with maxima of its planktic larvae in the preceding spawning season, and that periods of low benthic density correlated with preceding paucity of planktic larvae. He also noted that the amount of planktic larvae of a species was not directly related to the density of reproducing benthic individuals. Spawning of low-density benthic populations could result in either low or high numbers of larvae found in the water column, etc.

Thorson's (1950) summary of larval development provided explanations for many of the empirical observations of Blegvad. Thorson (1950 : fig. 2) showed that temporal variations in species with long planktic larval lives were greater than in species with short larval lives or direct development. He noted that larvae spending several weeks in the water column are affected by a number of purely pelagic environmental factors. These include losses within the larval population because of predation, fluctuations in their food supply of phytoplankton and movement away from suitable settling areas by currents. Such factors can affect the recruitment of benthic populations in the absence of change within the bottom environment.

Two important aspects of the Danish studies form a model for evaluating stratigraphic profiles of fauna.

1. In the modern examples, fluctuation in larval settlement and consequent benthic densities is not random. Several successive years of low larval numbers and small benthic populations alternate with several successive years of high larval densities and larger benthic populations.
2. Discrete events in the bottom environment or the size or presence of benthic populations are not the only factors influencing larval recruitment. Environmental factors in the water column, and not the bottom environment, may form a first-order control on the size of the larval population available for settling.

Comparison of the larval model with Ludlow sections

Species fluctuations in stratigraphic profiles of the *M. laevigata* and *G. obovata* Associations conform with the larval model in showing a lack of relation to bentonites, which represent discrete disturbances of the bottom environment. Note the cycles of relative abundance shown by *Protochonetes minimus* (taxon 26) in Fig. 25. Between 4·5 and 6 m in the section, *P. minimus* shows a cycle of high abundance. A bentonite caused a faunal destruction within this interval, but did not affect the cycle, for *P. minimus* maintains a nearly equal, high abundance both below and above the bentonite. Between 6 and 11 m in the section (Fig. 25), *P. minimus* shows a constant, low abundance. A second bentonite in this interval also fails to affect the occurrence of the species, which retains an equal, low abundance both below and above. Identical relations can be seen for many other brachiopod species in Figs 17, 22 and 25. Definite cycles of high and low abundances of particular species in the stratigraphic sections are virtually independent of the stratigraphic position of the bentonites.

These relations show that the stratigraphic fluctuations of species are independent of discrete changes in the bottom environment. They also show that presence of benthic populations of adults was not a necessary prerequisite for the settling of larvae of a particular species at the same site. Abundant adult populations, smothered by bentonites 2–5 cm thick, are followed by abundant larval settlement above the bentonite, without the possibility of direct attractive influence of pre-bentonite populations upon post-bentonite settlement of larvae. The best explanation for these phenomena, provided by the modern model, is that stratigraphic fluctuations in Ludlow species were controlled primarily by pelagic influences on larval survival, and not by benthic populations or events.

Brachiopod species in Ludlow distal shelf facies show a general stratigraphic pattern in which several metres of low-abundance occurrences alternate with intervals of higher abundance. No repetitive or successional relation is seen between the fluctuations of one species and those of others. This compares closely with the temporal patterns in modern species observed by Blegvad (1925, 1928). An important point, however, is the difference in time scale between Blegvad's observations and the probably longer spans of species fluctuations in the Ludlow sections. Walker & Bambach (1971) have emphasized that untransported assemblages of shells in fine-grained sediment represent a 'time-averaged' sample of many generations of individuals which lived at the same site. The fluctuations observed by Blegvad occurred only over several years, and the total pattern he observed of high and low abundances over 17 years would probably be preserved as a single averaged assemblage in a few mm of slowly-deposited distal shelf sediment. In spite of time-averaging, the cumulative effect of the type of fluctuation observed by Blegvad could be expressed in a stratigraphic section if the net average of fluctuations over a period of several hundreds or thousands of years differed from the average in a succeeding long period of time.

The model of pelagically-controlled larval effects provides a better explanation for the stratigraphic variations within Ludlow distal shelf communities than a model of ecological succession within the bottom environment. The time-scale of fluctuations seen in the Ludlow communities is not comparable with that known in modern examples. It is proposed, however, that time-averaging of fossil assemblages would grossly preserve, rather than completely obscure, the larvally-related temporal variation known in modern communities.

Biotic interaction in Ludlow communities

Predation

The foregoing analysis of stratigraphic patterns in Ludlow communities has reached negative conclusions regarding the existence of ecological succession, which implies a lack of the type of organism interactions and feedback which are an integral part of succession (Margalef 1968). Limited evidence does exist, however, for some direct interaction in Ludlow communities. One type of interaction is predation, evinced by a type of small, circular boring found in one valve of *Amphistrophia funiculata* and two of *Nuculites antiqua*. Indirect evidence, considered below, suggests that predation may have played a larger role in the structure of Ludlow communities.

In modern marine communities, predators are known to have an important function in damping temporal fluctuations in densities and equalizing competition for space among prey species (Blegvad 1928; Paine 1966). Jackson (1972) found a correlation between low-diversity bivalve communities with low predation rates, and high-diversity, offshore bivalve communities experiencing higher rates of predation from a greater number of predatory taxa. Jackson suggested that high rates of predation generally contribute to higher diversities in level-bottom communities.

Apart from rare asteroids, potential predators among the Ludlow fauna of the Welsh Borderland include cephalopods, gastropods and phyllocarid crustaceans. The diversity of these groups increases toward the lower parts of the Ludlow column, in the distal shelf facies with higher diversity bottom communities (see Jones & Woodward 1888–89 and Blake 1882, as well as data in Appendix 3). Ludlow communities may therefore show a correlation between predator diversity and diversity of prey species, like that discussed by Jackson (1972). Highest and most constant rates of predation in Ludlow distal shelf environments might also have contributed to the relatively predictable, low-amplitude fluctuations of brachiopod species. These suggestions, though tantalizing, must remain tentative on the basis of present data.

Encrustation

The chief form of biotic interaction recorded in Ludlow faunas is encrustation, primarily of brachiopods, gastropods and cephalopods by a number of bryozoans, serpulids, cornulites, auloporids and boring organisms of unknown affinity. Some of these organisms can be seen on examples of *Isorthis orbicularis* (Pl. 5, fig. 1) and *Protochonetes ludloviensis* (Pl. 5, fig. 2). Preliminary observations of encrustation show little selectivity of host shells by encrusting organisms. They are overwhelmingly found on the external surfaces of shells, suggesting that many settled when the host was alive. Within samples, 1% or fewer of brachiopod and mollusc shells are encrusted and the lowest frequencies of encrustation occur in the *G. obovata* Association.

Under favourable conditions, the use of organisms by other organisms as hard substrates can produce enough interaction to result in an ordered ecological succession. Shäfer (1970) has described such a case in modern seas, and Walker & Alberstadt (1975) described a succession involving encrusting relations in the Ordovician. Encrustation within Ludlow shelf communities never reached the intensity of interaction in which an ecological succession could proceed. This was probably because of continual sedimentation, ensuring that the hard substrates provided by brachiopod and mollusc shells were always isolated and only temporarily available for colonization.

Were Silurian communities depth-related ?

Depth relations in modern benthic communities

Before summarizing the conclusions and general implications of the analysis of Ludlow shelf faunas, it is appropriate to consider the question of the depth relation of Silurian communities, which has coloured palaeoecological study of this period since the work of Ziegler (1965). In exhaustive studies of the environmental relations of modern benthic communities, Dörjes (1972) and Parker (1975) have shown that water depth is only one of a large number of factors which correlate with community distributions. Dörjes (1972) identified bottom morphology, grain size, sedimentation processes, relation to wave base and food supply as important influences on shelf communities off Georgia. Parker (1975) demonstrated statistical correlations between community distributions and current strength, grain size, turbulence, chemical state of the bottom and light penetration in Hadley Harbor, Massachusetts.

These studies show that many of the environmental factors relating to modern benthic communities revolve around the dynamic state of the sediment bottom. Where such conditions parallel bathymetry, and sedimentary facies zones are orientated parallel to the coastline, modern communities tend to occur in similar depth-related bands (Dörjes 1971, 1972). Where zones of similar sedimentary facies and hydrographic conditions are not parallel to the coastline or bathymetric contours, benthic communities show a similar lack of depth relation (Dörjes *et al.* 1969, 1970). These observations provide an important model for depth evaluation of ancient communities. They show that consistent depth relations of benthic communities are not intrinsic, but may be either present or absent, depending on the distribution of a complex of hydrographic factors.

Upper Llandovery communities of the Welsh Borderland

Ziegler (1965) and Ziegler *et al.* (1968*a*, 1968*b*) presented a picture of five communities occurring in consistent depth-related bands in the Upper Llandovery of Wales and the Welsh Borderland. Recent work on the sedimentology of these deposits by Bridges (1975) indicates that the depth relations of these communities is not as consistent as has been supposed. For C_1 times, Ziegler *et al.* (1968*b* : fig. 13) showed the control for their parallel bands of communities in a small area between Wenlock Edge and the Breidden Hills. Bridges (1975 : fig. 11A) has shown that this area did not possess an even bathymetric gradient, but included a southward-facing peninsula on the site of the Long Mynd. A *Lingula* Community lived east of this peninsula in the shallow sands of a restricted marine embayment. *Pentamerus* and *Stricklandia* Communities on the southern and western sides of the peninsula lived on open marine sands. Bridges' data suggest that position landward or seaward of the Long Mynd peninsula was the most important factor relating to community distribution.

By C_5 to C_6 times, the Welsh Borderland shelf possessed a fairly even bathymetric gradient with coarse to fine-grained sediments occurring in parallel bands away from the shoreline (Bridges 1975). The shelf communities at this time were also arranged in subparallel bands (Bridges 1975: fig. 11B), and the community distributions shown by Ziegler *et al.* (1968*b*: fig. 14) were probably closely related to bathymetry. This situation follows from the modern observations, which show that depth-related conditions of sedimentation will result in depth-related community distributions.

General depth relations in Silurian communities

Like modern marine communities, those of the British Upper Llandovery appear to show variable relation to water depth, according to the orientation of sedimentation conditions. They do not provide evidence for any intrinsic depth zonation of Silurian bottom faunas, and their use as 'bathymetric standards' for the Silurian (Boucot 1975) is fallacious.

The relation between bathymetry and sedimentation conditions in determining Silurian community distributions can be shown by a comparison between a terrigenous shelf and a carbonate platform brachiopod association. The *Mesopholidostrophia laevigata* Association of the Welsh Borderland occupied terrigenous bottoms probably under several tens of metres of water. This depth range is indicated by the position of the community in the distal shelf end of Ludlow stratigraphic gradients, resemblance of its enclosing sediment to modern, offshore shelf deposits and the total absence of any nearby shoreline (Holland & Lawson 1963). Hurst (1975*b*: table 3) has described brachiopod assemblages of nearly identical generic content to the *M. laevigata* Association from the Ludlow-age Eke Beds of Gotland. The Eke Beds were deposited on a carbonate platform, and consist of argillaceous limestone with abundant calcareous algae. They underlie and possibly grade laterally into the Burgsvik Sandstone, a probably intertidal deposit. The Eke Beds can thus be considered as very shallow in nature, deposited beneath waters of possibly only a few metres in depth.

This example shows that similar generic associations of Silurian brachiopods lived at shallower depths on carbonate platforms than on terrigenous shelves. In the Welsh Borderland, the *M. laevigata* Association occupied an environment of relatively quiet water and low sedimentation rate. These conditions were met with in an offshore, relatively deep situation in the terrigenous shelf setting. On the carbonate platform of Gotland, however, such conditions of sedimentation appear to have occurred in much shallower water, because of the reduced influence of terrigenous sediment influx. Thus, the Gotland counterpart of the *M. laevigata* Association could inhabit shallower absolute depths.

Both the example given above and the review of British Upper Llandovery communities given here are completely in keeping with modern observations on communities and water depths. All community distributions relative to water depth, whether parallel or oblique to bathymetric contours, are essentially 'special cases' related to the local sedimentation and hydrographic conditions. Silurian communities may or may not be related to water depth, depending on these factors, and faunal data alone cannot be used to make bathymetric correlations between different times and places.

Summary and implications of Ludlow community organization

The environmental gradient and composition of fauna

Ludlow sections in the Welsh Borderland record a slow, terrigenous progradation over a marine shelf, interrupted locally by carbonate deposition. A general trend of shallowing, increase in grain size and sedimentation rate, increase in shell transport and increase in frequency and intensity of storm-sedimentation events is apparent from the base to the top of the Ludlow column. Except for carbonate interruptions, the Ludlow sections represent a vertically superposed gradient from distal shelf to proximal shelf environments. A shoreface environment is not preserved.

Articulate brachiopods are dominant in number of individuals, but not of species, through the broad range of shelf environments, decreasing in diversity from the distal to proximal shelf. Only in relatively high-stress shelf environments is the abundance of articulate brachiopods approached or surpassed by that of other groups. These environments include deoxygenated distal shelf muds, rapidly-deposited proximal shelf silts and the brackish-water facies of the Downtonian.

Bivalves are locally abundant in distal shelf muds and proximal shelf silts, but generally comprise a small proportion of individuals within communities. They decrease in diversity along the distal to proximal shelf gradient, with distal shelf communities characterized by very sporadic occurrence of a large number of bivalve species. Gastropods also decrease in diversity from distal to proximal shelf communities. They are consistently present, but seldom abundant. Cephalopods are represented by pelagic and nektobenthic forms. Pelagic forms are abundant in distal shelf sediments, while nektobenthic forms are found in consistent low abundance through the whole shelf transect, and were probably predators.

Corals, bryozoa and crinoids show a preferential occurrence in distal shelf silts, where sedimentation was slow, but periodic agitation occurred. They decrease in abundance into proximal shelf silts with relatively high sedimentation rates, and also become rare in distal shelf muds. Trilobites are most abundant and diverse in distal shelf muds, but extend in low abundance across the full range of shelf environments. Minor groups of arthropods, annelids, echinoderms and small conoidal shells occur sporadically through various communities.

Trophic structures in Ludlow shelf communities indicate a mixture of deposit feeding and suspension feeding, with both abundant infauna and epifauna. Except where bryozoa and crinoids were common, little stratification occurred among the epifauna, and most suspension feeding probably occurred 0–2 cm above the substrate.

Dominance of physical factors in Ludlow community organization

The physical environment appears to have been paramount over biotic factors in shaping community patterns within Ludlow sections. The basic number and level of discreteness of Ludlow communities is a product of the history of environmental change. Long-term persistence of major sedimentary and hydrographic conditions produced extended stratigraphic intervals with relatively constant faunal content. Shorter intervals of environmental change produced subordinate stratigraphic intervals of faunal alteration and gradations between communities. An alternation of these phenomena produced the major stratigraphic pattern of Ludlow communities in the Welsh Borderland.

Stratigraphic variation occurs within communities in parts of sections representing stability in major environmental conditions. This variation does not lead to any progressive biological accommodation or increase in species diversity, and does not correspond to models of ecological succession. It consists of extreme and unpredictable fluctuations in the abundance of individuals of species in proximal shelf communities. In distal shelf environments, the intracommunity variation occurs mainly as lower amplitude, predictable cycles in abundance of species. These cycles are independent of faunal destructions represented by bentonites and storm-deposited silts. The cycles of one species do not consistently relate to those of others, or to any consistent patterns in diversity variation. The total pattern of temporal variation within communities does not conform to the repetition involved in ecological succession. Environmental influences upon the survival of pelagic larvae, and not events or interactions in the bottom environment, are the best model for intracommunity variation in Ludlow sections.

Except for minor sediment conditioning, ecological succession was probably precluded in Ludlow shelf environments by a lack of biotic control over the physical environment. Continued sediment dilution of benthic populations would have prevented the concentrated use of other organisms as substrates, and confronted newly-recruited larvae, on the average, with the same type of sediment bottom occupied by their parents. Sediment dilution of organic remains would preclude the inheritance of accumulated biological information, as discussed by Margalef (1968), which is necessary for new generations to proceed beyond the organizational state of their predecessors. In this situation, only a change in the external environment can cause an alteration of community structure.

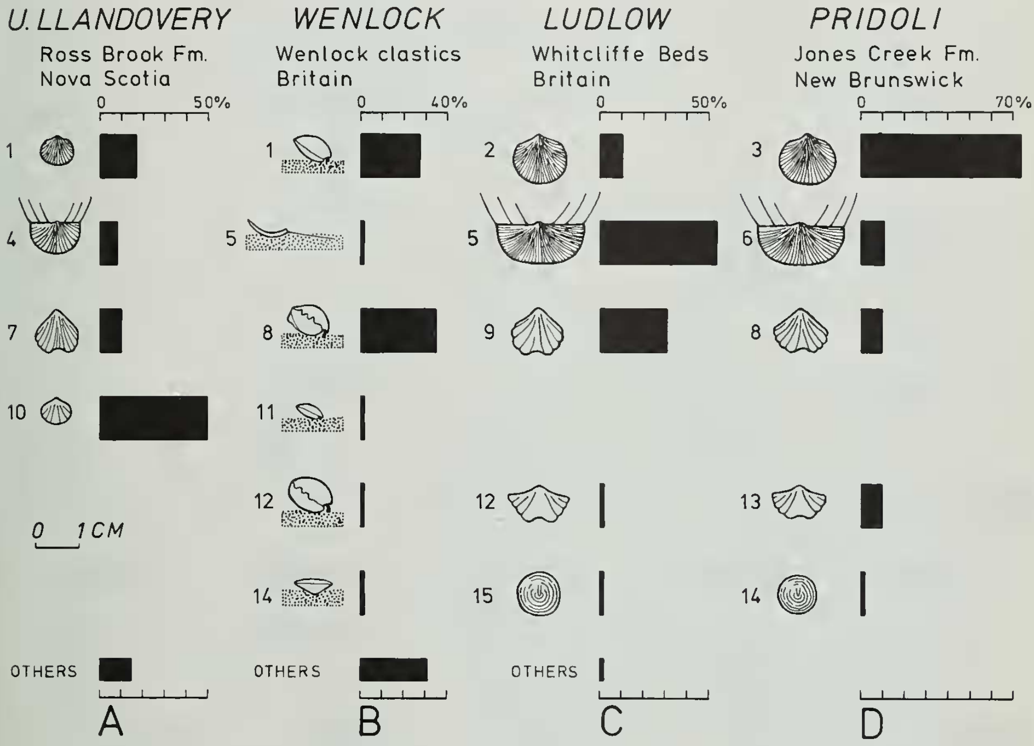

Fig. 26 Local examples of the *Salopina* Parallel Communities. Column B shows inferred life positions, and columns A, C and D show ventral views of the pedicle valve; low abundances are exaggerated to 2%. A – 'mixed *Salopina conservatrix* – *Eocoelia* Communities' of Watkins & Boucot (1975); B – *Salopina* Community of Calef & Hancock (1974); C – *Protochonetes ludloviensis* Association of this report; D – *Salopina submedia* Community of Watkins & Boucot (1975). 1 – *Salopina conservatrix* (McLearn); 2 – *S. lunata* (Sowerby); 3 – *S. submedia* (McLearn); 4 – *Protochonetes tenuistriata* (Hall); 5 – *P. ludloviensis* Muir-Wood; 6 – *Protochonetes* sp.; 7 – '*Camarotoechia*' *rossonia* McLearn; 8 – '*Camarotoechia*' spp.; 9 – '*C.*' *nucula* (Sowerby); 10 – *Eocoelia sulcata* (Prouty); 11 – *E. angelini* (Lindström); 12 – *Howellella elegans* (Muir-Wood); 13 – *Howellella* sp.; 14 – *Orbiculoidea* sp.; 15 – *O. rugata* (Sowerby).

The Ludlow fauna corresponds to the stability-time hypothesis in showing highest species diversity in the low-stress distal shelf environment. Rollins & Donahue (1975) have used such diversity relations to infer the existence of biological accommodation in such communities, a type of biotic interaction which can lead to progressive niche-partitioning and diversity increase. As Ludlow communities of distal shelf environments show no increase in diversity with temporal persistance of low-stress conditions, and do not show a successional pattern in cycles of species, they were probably not biologically-accommodated. If predation was important in the high-diversity communities, as suggested in the biotic interaction section, p. 249, it contributed to an overall stability in diversity and not a general increase.

An alternative explanation for high diversity in distal shelf environments is a simple correspondence of their physical conditions to the physiologic optima of the largest set of Ludlow shelf species. This relation has been expressed by Gibson & Buzas (1973) as the 'carrying capacity' of a particular environment, which remains constant through time.

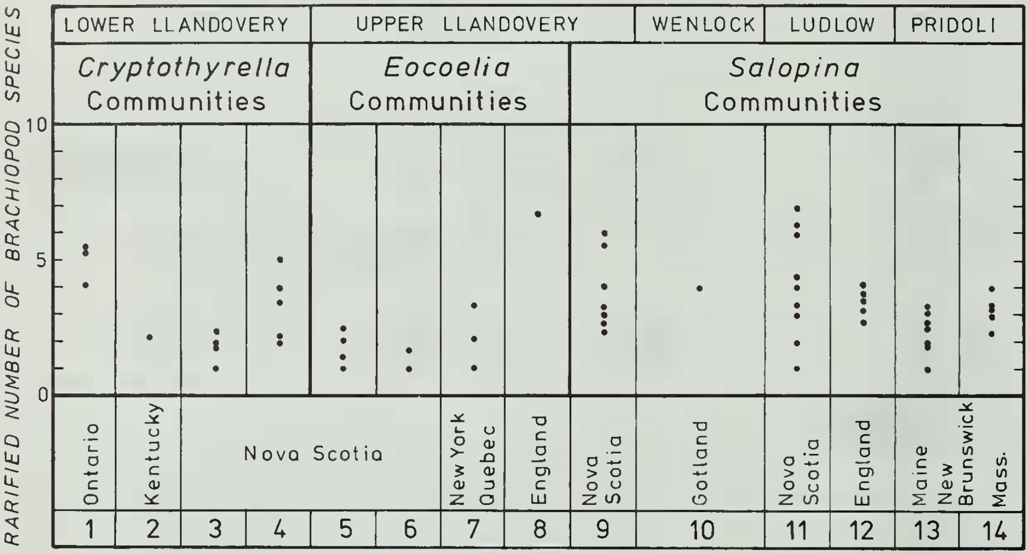

Fig. 27 Species diversity in parallel communities of the proximal shelf region. Each point represents a single sample, rarified to a diversity value at 50 individuals. In the list of data sources for this and following figures, 'USNM' indicates the number of a United States National Museum collection for which brachiopod data have been provided to the author by A. J. Boucot. These unpublished data are available on request. 1 – Manitoulin Dolomite, USNM 11582, 11584, 11585; 2 – Brassfield Limestone, USNM 11643; 3 – Beechhill Cove Formation, the *Cryptothyrella* Community of Watkins & Boucot (1975); 4 – Beechhill Cove Formation, the *Mendacella* Community of Watkins & Boucot (1975); 5 – Middle Member of Ross Brook Formation, the *Eocoelia* Community of Watkins & Boucot (1975); 6 – Upper Member of Ross Brook Formation, the *Eocoelia* Community of Watkins & Boucot (1975); 7 – Clemville Formation USNM 11107, Sodus Shale USNM 12018, Hickory Corners Limestone USNM 11897; 8 – Damery Beds, USNM 10217; 9 – Upper Member of Ross Brook Formation, the mixed *Salopina conservatrix – Eocoelia* Communities of Watkins & Boucot (1975); 10 – Klinteberg Beds, Hurst (1975*b*); 11 – Moydart Formation, the *Salopina submedia* – '*Camarotoechia*' aff. *planorugosa* Community of Watkins & Boucot (1975); 12 – Whitcliffe Beds, the *Protochonetes ludloviensis* Association of this report; 13 – Pembroke Formation, the *Salopina submedia* and *Protochonetes* Communities of Watkins & Boucot (1975); 14 – Jones Creek Formation, Newbury Volcanic Group, Ames Knob Formation and Pembroke Formation, the *Salopina submedia* Community of Watkins & Boucot (1975).

This discussion leads to the conclusion that both high diversity and low diversity communities in Ludlow sections were essentially under the external control of the physical environment. Physical environmental changes were necessary to effect any major change in faunal composition, population patterns or diversity of the shelf fauna. In Ludlow sections, changes in bottom type, sedimentation patterns and hydrographic conditions were the physical factors which exerted most influence upon fauna. In the absence of such changes, the same set of species continued colonizing the accumulating sediment bottoms, with pelagically-influenced variation in larval recruitment.

Consequence of physical control of Silurian shelf communities

The simple physically-controlled organization inferred for Ludlow shelf faunas has general implications for the Silurian record. There appears to be no intrinsic biotically-controlled change within Ludlow shelf communities. The consequence of this type of organization is expressed throughout Silurian time as relatively steady-state levels of diversity within level-bottom communities.

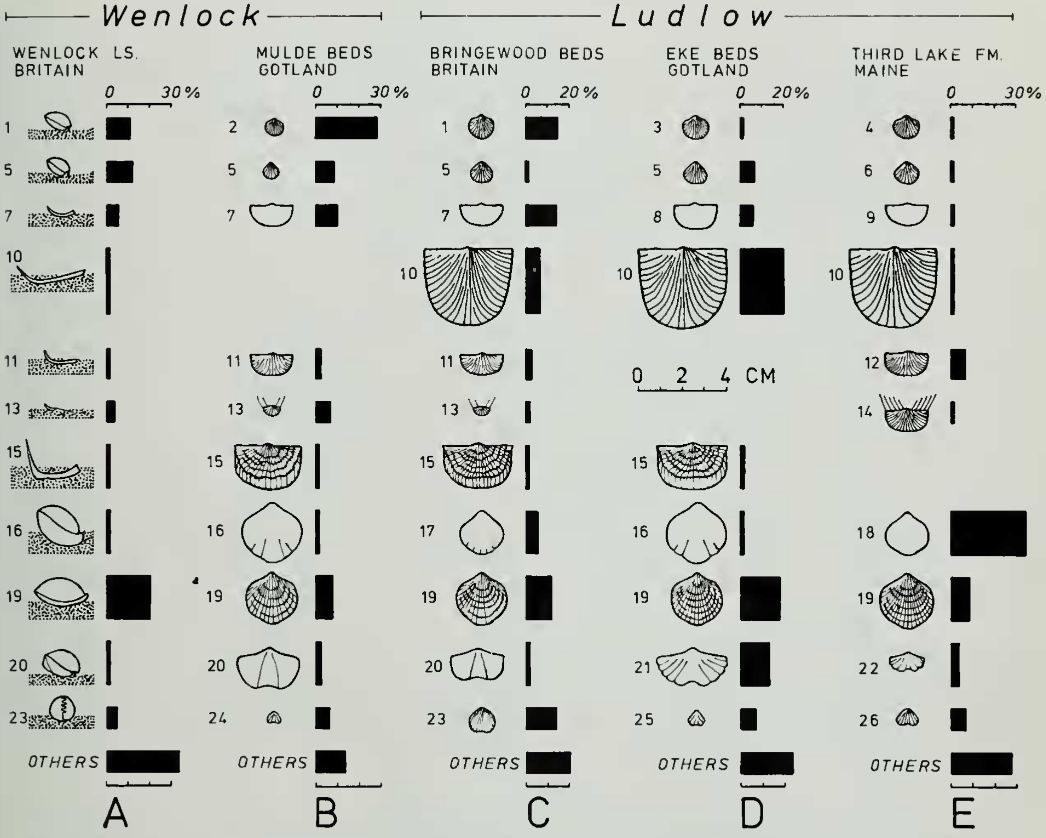

Fig. 28 Local examples of the Stropheodontid Parallel Communities, using data from A, Hurst (1975*c*); B, D, Hurst (1975*b*); C, this report; and E, USNM 11357, 11364, 11630. 1 – *Isorthis clivosa* Walmsley; 2 – *I. crassa* (Lindström); 3 – *I. canaliculata* (Lindström); 4 – *I.* cf. *arcuaria* (Hall & Clarke); 5 – *Dalejina hybrida* (Sowerby); 6 – *Dalejina* sp.; 7 – *Mesopholidostrophia laevigata* (Sowerby); 8 – *Brachyprion* sp.; 9 – *Mesopholidostrophia* sp.; 10 – *Strophonella euglypha* (Hisinger); 11 – *Amphistrophia funiculata* (M'Coy); 12 – *A.* cf. *funiculata* (M'Coy); 13 – *Protochonetes minimus* (Sowerby); 14 – '*Chonetes*' *jerseyensis* Hall; 15 – *Leptaena depressa* (Sowerby); 16 – *Gypidula galeata* (Dalman); 17 – *Gypidula lata* Alexander; 18 – *Gypidula* sp.; 19 – *Atrypa reticularis* (Linnaeus); 20 – *Eospirifer radiatus* (Sowerby); 21 – *Striispirifer striolatus* (Lindström); 22 – *Delthyris* sp.; 23 – *Sphaerirhynchia wilsoni* (Sowerby); 24 – *Ancillotoechia bidentata* (Hisinger); 25 – '*Camarotoechia*' *nucula* (Sowerby); 26 – *Ferganella* sp.

Parallel communities (Thorson 1957) are characterized by recurrent associations of genera on a nearly world-wide scale, and are well developed among Silurian brachiopods (Boucot 1975). Within Silurian proximal shelf faunas, a replacement from Lower Llandovery through to Pridoli times occurs from the *Cryptothyrella* Communities through *Eocoelia* Communities to *Salopina* Communities (Watkins & Boucot 1975). Some local examples of the *Salopina* Communities, including the *P. ludloviensis* Association of the Welsh Borderland, are shown in Fig. 26, and provide an illustration of the parallel community phenomenon. Like the *P. ludloviensis* Association, other local examples of these communities show a low diversity of brachiopods. This diversity pattern is shown in Fig. 27, and remains quantitatively stable throughout the Silurian.

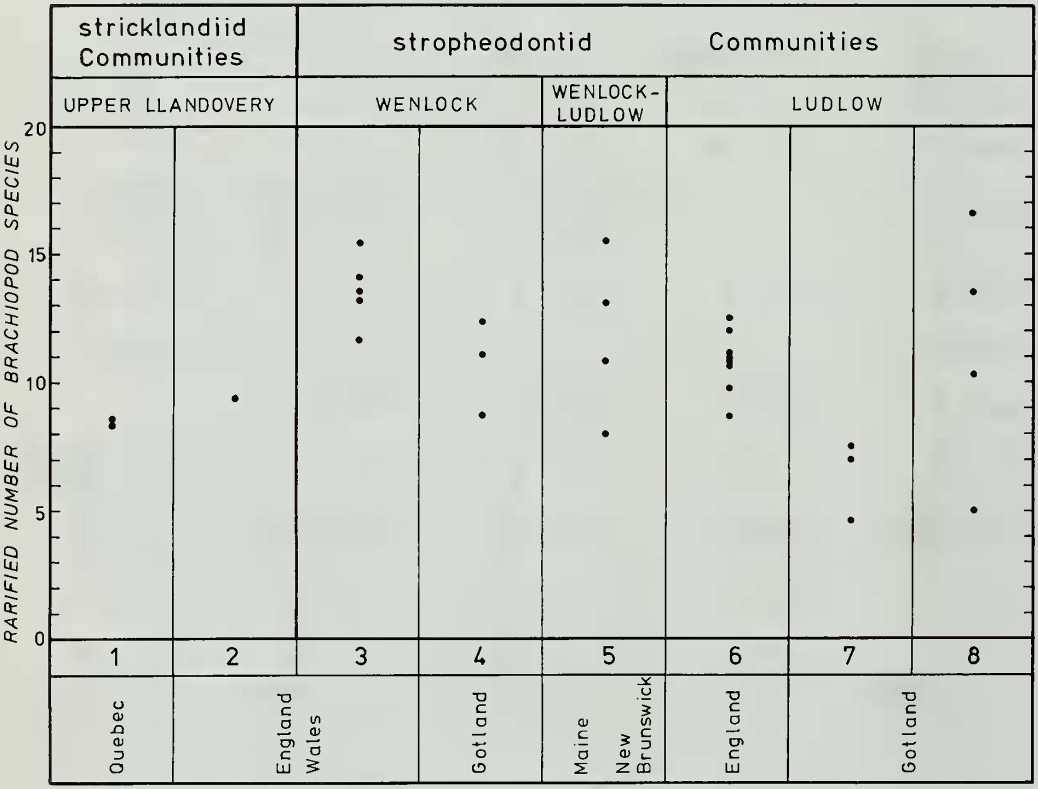

Fig. 29 Species diversity in the Stricklandiid and Stropheodontid Parallel Communities. Each point represents a single sample, from: 1 – La Vieille Formation USNM 11450, Val Brillant Quartzite USNM 11133; 2 – Wych Beds, the *Costistricklandia* Community of Ziegler *et al.* (1968*b*); 3 – Wenlock Limestone, the *Isorthis clivosa* Community of Hurst (1975*c*); 4 – Mulde Beds, Hurst (1975*b*); 5 – Third Lake Formation USNM 11357, 11364, 11630, Mascarene Series USNM 11917; 6 – Lower Bringewood Beds, the *Mesopholidostrophia laevigata* Association of this report; 7 – Hemse Beds, Hurst (1975*b*); 8 – Eke Beds, Hurst (1975*b*).

More diverse distal shelf or carbonate platform communities, like the *M. laevigata* Association, also exist as parallels throughout the Silurian. In the Llandovery, local examples are often dominated by stricklandiids (Ziegler *et al.* 1968*a*), and in the post-Llandovery, stropheodontid brachiopods are one of the characteristic forms. The Stropheodontid Parallel Communities show striking similarities between different areas and times, and are illustrated in Fig. 28. Diversity of these communities is plotted in Fig. 29, and also shows a general stable level throughout Silurian time.

The *Dicoelosia* Communities are another group of parallel associations among Silurian brachiopods. This suite of dominantly distal shelf, muddy bottom communities has been named the *Dicoelosia–Skenidioides* Community Group by Boucot (1975), and is represented by the *G. obovata* Association in the Ludlow of the Welsh Borderland. Although brachiopod diversity in these communities is highly variable, a plot through Silurian time shows a general stability in number of species present (Fig. 30).

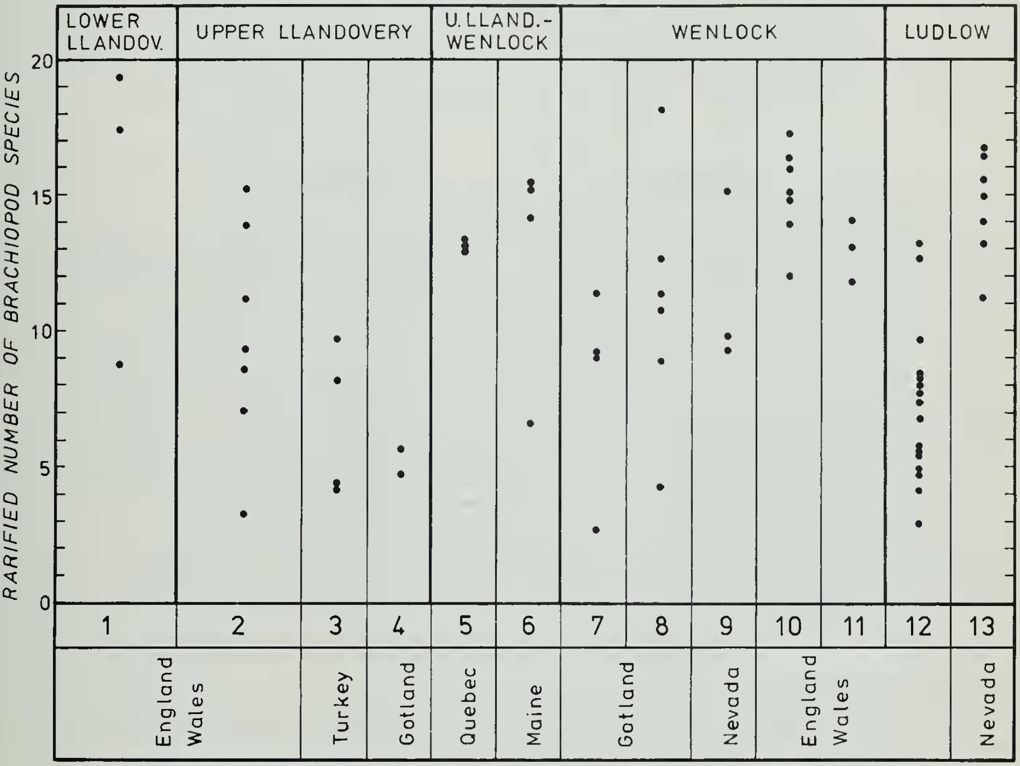

Fig. 30 Species diversity of the *Dicoelosia* Parallel Communities. Each point represents a single sample, from: 1 – Gasworks Mudstone USNM 10509, siltstone near Meifod, Temple (1970), limestone bands at Keisley, Temple (1968); 2 – C_1 to C_6 age beds, USNM 10259, 10260, 10514, 10512, 10272, 10257, 10258; 3 – Umur-Dere-Folge (A III 3), USNM 10678, 10679, 10681, 10686; 4 – Lower Visby Beds, Hurst (1975*b*); 5 – Pointes-aux-Trembles Formation, USNM 11173, 11490, slates at Lac des Eaux Mortes USNM 11194; 6 – Perham Formation 11174, 13029, Dennys Formation USNM 11850, 11870; 7 – Upper Visby Beds, Hurst (1975*b*); 8 – Högklint Beds, Hurst (1975*b*); 9 – Hidden Valley Dolomite, USNM 12879, 13617, 17417; 10 – Woolhope Limestone, *Eoplectodonta duvalii* Community of Hurst (1975*c*); 11 – Wenlock Limestone, *E. duvalii* Community of Hurst (1975*c*); 12 – Middle Elton Beds, *Glassia obovata* Association of this report; 13 – Roberts Mountains Formation, Johnson *et al.* (1976).

The steady-state diversities within Silurian shelf communities of brachiopods through tens of millions of years has been previously discussed by Boucot (1975). It provides direct evidence that biological accommodation leading to progressive diversity increase did not occur in either low diversity or high diversity communities through Silurian time. The phyletic evolution in Silurian brachiopods must therefore have primarily involved niche replacements within stable community structures, rather than niche diversification or partitioning. The analysis of Ludlow shelf faunas in the Welsh Borderland suggests that this long-term stability of community structure resulted from a primary control of faunal patterns by the external physical environment.

Acknowledgements

I am grateful to J. M. Hurst for invaluable encouragement through this project, and joint participation in the study of *Isorthis*. I also wish to thank C. J. Aithie, W. B. N. Berry, A. J. Boucot, A. Hallam, A. P. Heward, R. A. Hewitt, J. G. Johnson, M. Lockley, W. S. McKerrow, R. M. Sykes and A. Williams for help in many ways. £200 toward the work was provided by the Burdett-Coutts Foundation of the University of Oxford, and facilities for preparing the manuscript were made available by the University of California Museum of Paleontology, Berkeley.

Appendix 1. Location of measured sections

Area 1. Millichope

Section 1B. This section is 4·1 m thick, in an old quarry on a hillside due N of Holloway Farm, SO 53608944. It is entirely within the Upper Leintwardine Beds (Shergold & Shirley 1968), and sample numbers 1B1–1B6 were assigned.

Section 1C. This section is 8·1 m thick, in very low, overgrown exposures on W side of a lane bordering Millichope Park, 126 m south of junction of this lane with Holloway to Upper Millichope road, SO 52888900. Samples 1C1–1C2 were collected from the Upper Leintwardine Beds, and samples 1C3–1C8 from the Lower Leintwardine Beds.

Section 1D. 3·9 m of strata measured in a small quarry on N side of Holloway to Upper Millichope road, directly opposite house at entrance to Millichope Park, SO 52748911. Assigned to the Lower Bringewood Beds (Shergold & Shirley 1968). Samples 1D1–1D10 were collected.

Section 1E. 15·8 m of strata measured in stream section on NE side of Holloway to Upper Millichope road near Upper Millichope, between SO 52048959 (base of section) and SO 52128943 (top of section). The section is within the Middle Elton Beds, and samples 1E1–1E16 were collected.

Area 2. Ludlow

Section 2A. 0·6 m of strata measured on N bank of 'Ludford Lane', 106 m W of its junction with the A49, SO 51157413. Sample 2A1 is from the Ludlow Bone Bed, and 2A2 and 2A3 from the underlying Upper Whitcliffe Beds.

Section 2B. 10·4 m of strata measured at loc. 6 of Holland *et al.* (1963), the type section for the Upper Whitcliffe–Lower Whitcliffe boundary, SO 50967414. Samples 2B1–2B7 were collected from the Upper Whitcliffe Beds, and 2B8–2B9 from the Lower Whitcliffe Beds.

Section 2C. 23·8 m of strata measured at locs 3 and 8 of Holland *et al.* (1963), including the type boundaries for the bases of the Lower Whitcliffe Beds and Upper Leintwardine Beds, SO 50717428 (base of section) to SO 50717425 (top of section). Samples 2C1–2C9 were collected from the Lower Whitcliffe Beds, 2C10–2C15 from the Upper Leintwardine Beds and 2C16–2C19 from the Lower Leintwardine Beds.

Section 2D. 17·8 m of strata measured at loc. 30 of Holland *et al.* (1963), the type section for the Lower Leintwardine–Upper Bringewood boundary, SO 49537255. Samples 2D1–2D11 were collected from the Lower Leintwardine Beds, 2D12–2D15 from the Upper Bringewood Beds.

Section 2E. 3·4 m of strata measured in a small cutting on S side of the Whitcliffe Spur Road, and in low dip exposures immediately adjacent. Section at W border of landslip, SO 47227376. It is within the Upper Bringewood Beds, and samples 2E1–2E3 were collected.

Section 2F. 5·1 m of strata measure on N side of forestry track in Mary Knoll Valley, at type section for Lower Bringewood–Upper Elton boundary (Holland *et al.* 1963: fig. 12), SO 48737292. Samples 2F1–2F3 were collected from the Lower Bringewood Beds, and 2F4–2F5 from the Upper Elton Beds. This section is very poorly exposed, and the boundary of these units was covered at the time of observations.

Section 2G. 0·9 m of strata measured in small exposure on S side of Old House Road at loc. 30 of Lawson (1973*b*), SO 48327257. This exposure is in the Upper Elton Beds, and was assigned sample number 2G1.

Section 2H. 2·6 m of strata measured in small cutting on N side of Hazel Coppice Road, at W end of loc. 27 of Lawson (1973*b*), SO 47597350. The section is in the Upper Elton Beds, and sample numbers 2H1–2H4 were assigned.

Section 2I. 3·6 m of strata measured in cutting at junction of forestry roads on W side of High Vinnals, loc. 70 of Lawson (1973*b*), SO 47507161. The section is in the Middle Elton Beds, and samples 2I1–2I6 were collected.

Section 2J. 7·2 m of strata measured in deep double-sided cutting on S side of Goggin Road at loc. 69 of Lawson (1973*b*), SO 47437171. The section is near the base of the Middle Elton Beds, and samples 2J1–2J12 were collected.

Area 3. Woodbury Quarry

Section 3A. A single section, 163 m thick, measured in Woodbury Quarry, from SO 74256363 (top of section) to SO 744637 (base). Samples 3A1–3A26 were collected from the Whitcliffe Beds, 3A27–3A29 from the Upper Leintwardine Beds, 3A30–3A48 from the Lower Leintwardine Beds, 3A49–3A51 from the Upper Bringewood Beds and 3A52–3A120 from the Lower Bringewood Beds. All units but the Whitcliffe Beds were being actively quarried, and the amount of Lower Bringewood Beds exposed from time to time varied. Small faults, of undetermined displacement, occur at 65·87 m and 71·45 m above base of section.

Area 4. Ledbury

Section 4A. 52·5 m of strata measured at N end of Frith Wood, in section described by Penn *et al.* (1971 : fig. 9). The base of this section, SO 72304024, is located at SW corner of junction of forestry tracks named Top Walk and Godwin's Rise. From this point, the section was measured downhill (SW) along S bank of Godwin's Rise, for 280 m along this track; top of section SO 72064011. Samples 4A1–4A26 were collected from the Whitcliffe Beds, 4A27–4A29 from the Upper Leintwardine Beds, 4A30–4A54 from the Lower Leintwardine Beds and 4A55–4A58 from the Upper Bringewood Beds.

Section 4B. 77·6 m of strata measured in old quarry on N side of Knapp Lane, from SO 71403857 (base of section) to SO 71313858 (top), immediately outside Ledbury. Samples 4B1–4B26 were collected from the Lower Bringewood Beds and 4B27–4B35 from the Upper Elton Beds. Several small faults, of undetermined displacement, occur between 36 m and 55 m above base of section.

Section 4C. 5·8 m of strata measured at loc. 22 of Penn *et al.* (1971 : fig. 8), in NE bank at junction of two lanes, SO 71523857. This section is in the Middle Elton Beds, and samples 4C1–4C4 were collected.

Area 5. Perton

Section 5A. 6·1 m of strata measured in southernmost of series of old quarry faces S of Perton, on E side of Perton Lane, SO 59694031. This section is shown at loc. 2 by Curtis *et al.* (1967 : fig. 5). It is in the Upper Whitcliffe Beds, and samples 5A1–5A6 were collected.

Section 5B. 2·9 m of strata measured in small cutting on E side of Perton Lane, immediately S of where a footpath meets the lane, SO 59674033. This section is shown as loc. 3 by Curtis *et al.* (1967 : fig. 5). It is in the Lower Whitcliffe Beds, and samples 5B1–5B3 were collected.

Section 5C. 13·5 m of strata measured in overgrown exposures in E bank of Perton Lane, from SO 59694024 (top of section) to SO 59614013 (base). Samples 5C1–5C5 were collected from the Lower Whitcliffe Beds, 5C6–5C8 from the Upper Leintwardine Beds and 5C9–5C13 from the Lower Leintwardine Beds. The Upper Leintwardine Beds in this section are shown as loc. 4 by Curtis *et al.* (1967 : fig. 5), at SO 59634018.

Section 5D. 18·4 m of strata measured in Perton Quarry, on the main W face (Pl. 3, fig. 2) and an upper SW face immediately adjacent, SO 59523995. Samples 5D1–5D10 were collected from the Lower Leintwardine Beds, and 5D11–5D12 from the Upper Bringewood Beds.

Section 5E. 15·4 m of section measured S of Perton Quarry, in discontinuous exposures in E bank of Perton Lane from SO 59583992 (top of section) to SO 59613977 (base). This section is in the Lower Bringewood Beds, and samples 5E1–5E10 were collected.

Section 5F. 2·7 m of strata measured in small exposures in both E and W banks of Perton Lane immediately NW of farmhouse at Copgrove, SO 59643964. This section is in the Lower Bringewood Beds, and samples 5F1–5F3 were collected.

Section 5G. 7·4 m of strata measured in small cutting and other limited exposures in W bank of lane between Tower Hill and Wootton, at a bend in lane at SO 59253950. This section is shown as loc. 7 by Curtis *et al.* (1967 : fig. 5). Sample 5G1 was collected from the Lower Bringewood Beds and 5G2–5G7 from the Upper Elton Beds.

Section 5H. 7·6 m of strata measured in E bank of lane between Tower Hill and Wootton at SO 59223940. This section is in the Upper Elton Beds, and samples 5H1–5H7 were collected.

Section 5I. 38·6 m of strata measured in E bank of lane between Tower Hill and Wootton, between SO 59223935 (top of section) and SO 59233918 (base). These exposures are interrupted by the drive into Tower Hill Cottage (which is not actually on Tower Hill). The section is in the Middle Elton Beds, and samples 5I1–5I29 were collected.

Appendix 2. Reliability of faunal sampling

Definitions and procedures

As discussed earlier, density measurements are not adequate for standardization of palaeontological samples from a variety of sedimentary facies, and counts of numbers of individuals (as defined in methods section, pp. 178–9) have been used for this purpose. Samples processed for this project represent a variety of rock volumes and vary in content from 10 to 700 individuals. In the following discussions, 'sample size' refers exclusively to the number of individuals per sample. Representative sample sizes are given in Appendix 3, Tables 17–20. Most samples contained 50–75 individuals.

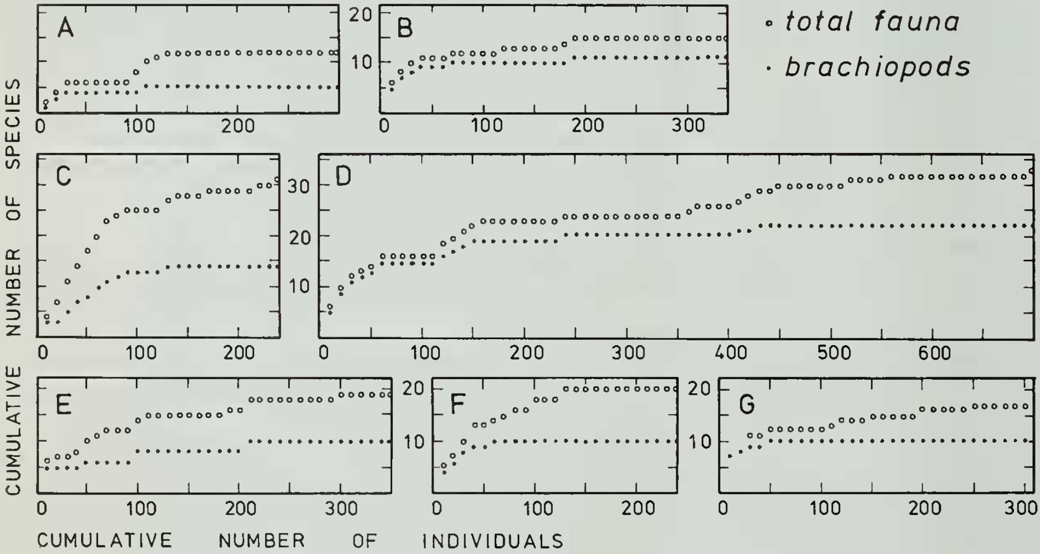

Fig. 31 Relation of number of individuals counted to number of species obtained in single samples. A – sample 4A7, *Protochonetes ludloviensis* Association; B – sample 4A44, upper phase of *Sphaerirhynchia wilsoni* Association; C – sample 4B31, 'transition fauna'; D – sample 4C1, *Glassia obovata* Association; E – sample from the Lower Leintwardine Beds at Chance's Pitch (SO 750402), upper phase of *S. wilsoni* Association; F – sample 4A29, *Shaleria ornatella* Association; G – sample 4A28, *S. ornatella* Association.

Relation of sample size to measured properties of samples was evaluated by the following method. In each of eight large samples from a variety of communities and sediments, all fossil specimens were listed in the order in which they appeared on fissile surfaces during processing of the rock. This order of appearance is considered random. From such lists, the content of each sample was calculated separately at 10-individual intervals for sample sizes ranging from 10 to over 240 individuals. The data were used to construct curves for each sample showing changes in measured properties with change in sample size. This procedure is the basis for the following discussions.

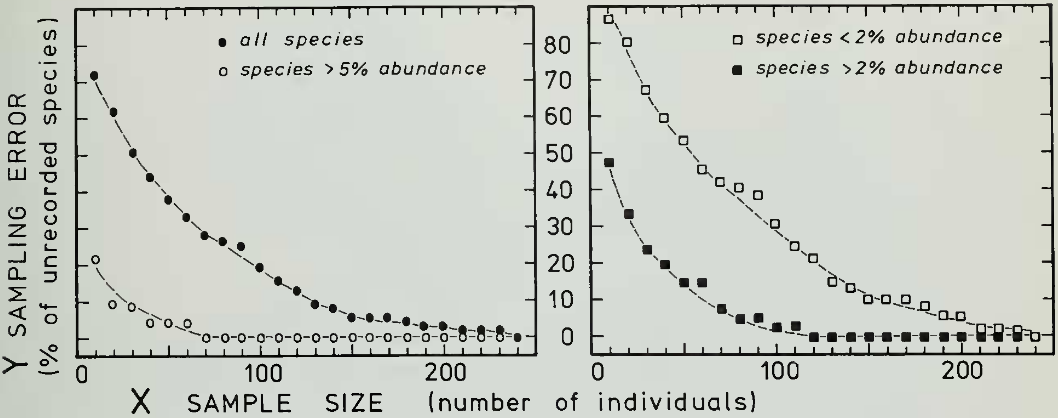

Fig. 32 Percentage of unrecorded species at different sample sizes, where 240 individuals are arbitrarily considered to yield 100% of species. These curves are based on data in Fig. 31. The sampling error, *Y*, was calculated as follows: samples A, B, C, E, F, & G of Fig. 31 yielded 104 total species at sample sizes of 240 individuals (62 species <2% relative abundance, 42 species >2%, 23 species >5%). At counts of 10, 20, 30 individuals, etc., the number of species recorded in these samples was divided by the number at 240 individuals. This value was then subtracted from 100% to obtain *Y*. See text for discussion of results.

Presence/absence criteria for species

Fig. 31 shows the increase in number of species obtained with increasing sample size. Beyond 200 individuals, most species curves remain constant or increase at a very slow rate. The number of species obtained at 240-individual sample size was arbitrarily assigned a value of 100% for comparison with species numbers in smaller samples. Results of this procedure are given in Fig. 32. Species with relative abundances above 5%, which include those used for the characterization of communities, were obtained at all sample sizes above 70 individuals. Rarer species, especially those comprising less than 2% of fauna in samples, had a much poorer rate of recovery (Fig. 32). Failure to record these species at sample sizes below 200 individuals is not conclusive evidence of their absence from any given area of rock.

Measurement of relative abundance

Relative abundances for each form within samples are defined, as a percentage, as the number of individuals of the form divided by the total number of individuals in a sample. Fig. 33 shows the relation between increasing sample size and measurements of relative abundance. Relative abundance values for each species show fluctuations within the same sample between sample sizes of 10 and 150 individuals, and stabilize above 200 individuals. Absolute stabilization is not seen in the curves, however, and measurement of relative abundance beyond the nearest 1% is not valid for even the largest samples used here.

The following method was used to compare the reliability of relative abundance measurements at different sample sizes. The error in measurement of the relative abundance of any species is arbitrarily set at 0 in a sample size of 200 individuals. The difference between the relative abundance for a species in a 200-individual sample and its relative abundance at any other sample size is *d*. Twenty-one species, all with relative abundances over 5%, were used in calculating *d* values at 24 sample sizes from 10 to 240 individuals.

The average error in relative abundance, specific for a particular sample size, is designated as *Y*, and calculated as:

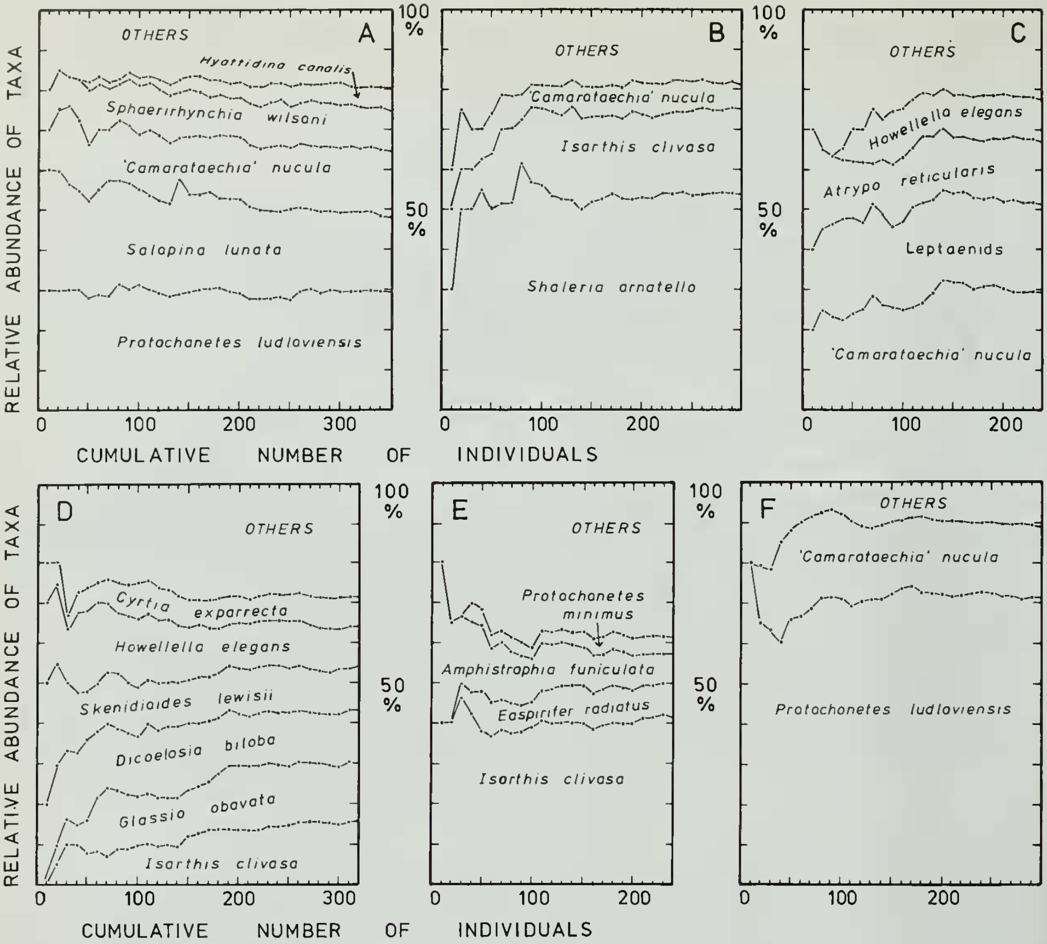

Fig. 33 Relation of increasing sample size to the measurement of relative abundances. A – sample from Chance's Pitch; B – sample 4A28; C – sample 4A29; D – sample 4C1; E – sample 4B31; F – sample 4A7.

$$\frac{\sum |d|}{21} = Y$$

Plots of Y values against sample size are shown in Fig. 34. As an absolute value, the average error in measurement of relative abundance per species is 3% or less at sample sizes above 50 individuals. These results indicate that once a species has been recorded in samples above this size, the measurement of its relative abundance is fairly accurate.

Appendix 3. Faunal lists

The following tables present a small part of the quantitative faunal data which form the basis for this study. The full data are deposited in the Library of the British Museum (Natural History), Cromwell Road, London. They comprise 54 typewritten sheets giving faunal counts for 417 samples in the measured sections. These data should be consulted by anyone wishing to make comparisons with the community analysis presented here. Tables 17–20 are extracts from the complete data, and show the format used.

Tables 15 and 16, which follow, record the total faunal content of each Association, based on total counts for all their assigned samples. These tables tell nothing of the variability within the associations,

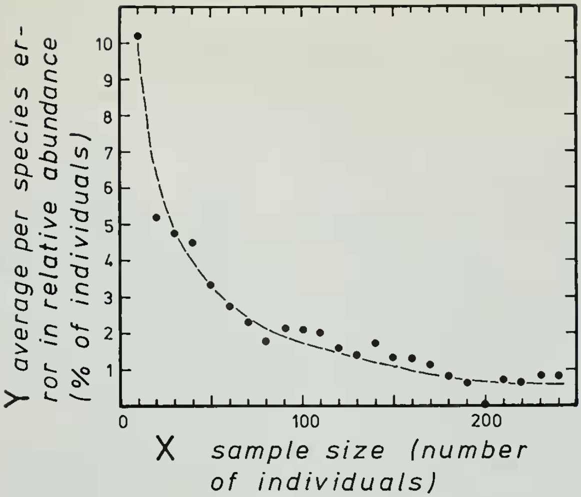

Fig. 34 Average error in measurements of relative abundance, based on calculations discussed in text. The curve was constructed for species whose relative abundances are above 5%. The error in measuring relative abundances for rarer species would fall below the curve.

and should not be taken as a 'fixed' definition of an association. Tables 17–20 give selected sample-by-sample data for some of the major associations, and provide examples of the basic data used in constructing the graphic faunal profiles.

Table 15 Cumulative faunal content for samples assigned to the following associations: Go1 – *G. obovata* (laminated shale facies); Go2 – *G. obovata* (mudstone facies); tr – transition fauna; M1 – *M. laevigata*; lpSw – lower phase of *S. wilsoni*; AC – *A. reticularis* – coral. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals

Association	Go1	Go2	tr	M1	lpSw	AC
ANTHOZOA						
Favosites cf. *forbesi* (Edwards & Haime)	–	–	–	–	1	–
Rhabdocyclus porpitoides (Lang & Smith)	–	–	–	7	1	–
solitary trochoid corals	–	24	12	141	34	100
syringoporid	–	1	5	3	–	–
BRYOZOA	–	1	72	597	285	122
BRACHIOPODA						
Aegiria grayi (Davidson)*	×	14 000	20	–	–	–
ambocoelid	–	–	–	4	3	–
Amphistrophia funiculata (M'Coy)	–	1	36	225	11	–
Atrypa reticularis (Linnaeus)	–	3	66	867	312	347
'*Camarotoechia*' *nucula* (J. de C. Sowerby)	–	–	–	31	102	23
Coolinia pecten (Linnaeus)	–	–	–	1	4	2
Craniops implicata (J. de C. Sowerby)	–	239	15	130	52	–
Cyrtia exporrecta (Wahlenberg)	–	42	3	1	–	–
Dalejina hybrida (J. de C. Sowerby)	–	53	28	119	170	–
Dayia navicula (J. de C. Sowerby)	–	1	193	3	–	–
Delthyris sp.	–	–	–	1	–	–
Dicoelosia biloba (Linnaeus)	–	116	–	–	–	–
Eospirifer radiatus (J. de C. Sowerby)	–	5	60	70	3	1

Table 15 continued

Association	Go1	Go2	tr	M1	IpSw	AC
Gasconsia sp.	–	–	–	2	–	–
Glassia obovata (J. de C. Sowerby)	27	603	–	–	–	–
Gypidula lata Alexander	–	37	10	448	78	2
Howellella elegans (Muir-Wood)	1	206	162	355	1223	10
Hyattidina canalis (J. de C. Sowerby)	–	–	–	–	1	1
Isorthis clivosa Walmsley	–	1675	223	1041	–	–
Isorthis orbicularis (J. de C. Sowerby)	–	–	–	–	265	5
Kirkidium knightii (J. Sowerby)	–	–	–	3	1	–
Leangella segmentum (Lindström)	–	9	–	–	–	–
Leptaena depressa (J. de C. Sowerby) and *Lepidoleptaena* sp.	–	5	4	165	85	26
Leptostrophia filosa (J. de C. Sowerby)	–	1	21	584	36	–
Lingula lata J. de C. Sowerby*	1	1	–	–	–	–
Lingula lewisii J. de C. Sowerby	–	19	7	54	19	3
Lingula n. sp.	–	10	–	–	–	–
Ludfordina pixis Kelly	–	192	–	–	–	–
Meristina obtusa (J. de C. Sowerby)	–	–	–	1	–	–
Mesopholidostrophia laevigata (J. de C. Sowerby)	–	34	69	1053	63	2
Nucleospira pisum (J. de C. Sowerby)	–	9	28	–	–	–
Orbiculoidea rugata (J. de C. Sowerby)	–	2	1	4	4	5
Parastrophinella sp.	35	133	–	–	–	–
Plagiorhyncha sp.	10	353	–	–	–	–
Protochonetes ludloviensis Muir-Wood	–	–	–	2	54	33
Protochonetes minimus (J. de C. Sowerby)	2	217	28	125	–	–
? *Protozeuga* sp.	–	87	3	–	–	–
Resserella sabrinae nunfieldensis Hurst	3	13	–	–	–	–
Resserella sp.	–	–	–	2	–	–
Rhynchospirina sp.	–	–	–	4	10	–
Salopina lunata (J. de C. Sowerby)	–	–	–	–	3	–
'*Schuchertella*' sp.	–	14	10	90	4	–
Shagamella ludloviensis Boucot & Harper*	–	145	3152	724	73	5
Shaleria ornatella (Davidson)	–	–	–	41	17	4
Skenidioides lewisii (Davidson)	1	306	80	7	–	–
Sphaerirhynchia wilsoni (J. Sowerby)	–	–	34	1082	872	48
Strophonella euglypha (Hisinger)	–	27	13	493	20	3
indeterminate rhynchonellides	–	1	3	14	28	–
indeterminate spiriferides	–	–	6	95	13	3
indeterminate brachiopods	4	–	–	–	–	–
GASTROPODA						
Bellerophon baccatus Reed	–	2	–	–	–	–
Bembexia lloydii (J. de C. Sowerby)	–	20	14	34	51	4
Bucanopsis expansus (J. de C. Sowerby)	–	–	1	1	5	–
Cymbularia cf. *fastigata* (Lindström)	6	55	4	–	–	–
Euomphalus sp.	–	10	–	38	14	1
gastropod sp. A	2	3	–	–	–	–
gastropod sp. B	–	1	–	–	–	–
Leptozone striatissima (Salter)	–	21	8	21	33	–
Loxonema sinuosa (J. de C. Sowerby)	18	32	–	1	–	–
murchisoniacean sp. B	–	–	–	3	1	–
Oriostoma sp.	–	1	–	24	28	45
platyceratacean sp. A	–	–	–	1	–	–
pleurotomariacean sp. A	–	17	–	–	–	–
pleurotomariacean sp. B	1	11	–	–	–	–

Table 15 continued

Association	Go1	Go2	tr	M1	lpSw	AC
Sinuspira stokei (Longstaff)	4	22	–	–	–	–
Sphenosphaera sp.	3	6	–	–	–	–
Temnodiscus salopiensis Reed	–	1	–	–	–	–
indeterminate bellerophontaceans	–	1	1	2	1	1
indeterminate high-spired gastropods	–	–	4	8	5	–
indeterminate gastropods	6	48	5	25	28	21
BIVALVIA						
Actinopteria sowerbyi (M'Coy)	–	2	–	20	7	–
bivalve sp. A	–	–	1	2	–	–
bivalve sp. B	1	1	–	–	–	–
bivalve sp. C	–	–	–	2	2	–
bivalve sp. F	–	–	–	5	1	–
Buchiola sp.*	3	–	–	–	–	–
Butovicella migrans (Barrande)*	13	9	–	–	–	–
Cardiola interrupta (J. de C. Sowerby)*	10	21	4	–	1	–
Conocardium sp.	–	1	1	–	–	–
Cypricardinia subplanulata Reed	–	–	2	39	8	–
'*Cyrtodonta*' *perovalis* (Salter)	–	9	7	2	2	–
cyrtodontid sp. A	–	–	–	1	–	–
Dualina striata (J. de C. Sowerby)*	6	12	–	–	–	–
Goniophora cymbaeformis (J. de C. Sowerby)	–	12	12	8	7	–
grammysid sp. A	–	35	9	–	–	–
Grammysioidea sp.	–	–	–	2	–	–
Leptodesma ampliata (Phillips)	–	2	1	1	–	–
Modiolopsis consors Reed	–	4	3	–	–	–
Modiolopsis solenoides (J. de C. Sowerby)	–	2	2	2	–	–
modiomorphid sp. A	–	–	1	–	3	–
modiomorphid sp. B	–	–	1	2	2	–
modiomorphid sp. C	–	–	1	1	–	–
modiomorphid sp. D	–	9	–	–	–	–
modiomorphid sp. E	–	3	8	–	–	–
modiomorphid sp. F	–	–	1	–	–	–
Mytilarca siluriana Reed	–	13	14	8	6	–
Nuculites antiqua (J. de C. Sowerby)	–	–	–	9	10	–
Nuculites pseudodeltoideus Reed	–	4	1	–	–	–
Nuculites woolhopensis Reed	9	109	9	–	–	–
Orthonota rigida (J. de C. Sowerby)	–	5	5	11	5	–
Orthonota sp. A	–	–	1	–	–	–
Palaeopecten danbyi (M'Coy)	–	–	3	5	1	–
'*Paracyclas*' *insueta* Reed	–	–	2	5	2	–
Praectenodonta ludensis (Reed)	1	8	2	–	–	–
Praenucula sp.	9	91	1	–	–	–
Pteronitella retroflexa (Wahlenberg)	–	–	–	3	–	3
Ptychopteria tenuistriata (M'Coy)	–	–	–	4	1	–
Sedgwickia amygdalina (J. de C. Sowerby)	–	–	–	5	5	–
Similodonta sp.	–	–	1	4	–	–
Slava fibrosa (J. de C. Sowerby)*	3	–	–	–	–	–
indeterminate pteriaceans	–	2	4	–	–	–
indeterminate bivalves	7	32	31	33	11	2
CEPHALOPODA						
'*Cyrtoceras*' *laevis* (J. de C. Sowerby)	–	16	1	–	–	–
Cyrtocycloceras tenuiannulatum (M'Coy)	1	7	1	6	1	–

Table 15 continued

Association	Go1	Go2	tr	M1	lpSw	AC
Cyrtocycloceras tracheale (J. de C. Sowerby)	6	15	1	–	5	1
Dawsonoceras annulatum (J. Sowerby)	–	2	–	–	–	–
Kionoceras caniculatum (J. de C. Sowerby)	4	2	2	1	6	4
Kionoceras sp. B	–	2	2	6	2	–
'*Orthoceras*' *dimidiatum* (J. de C. Sowerby)*	×	×	3	–	–	–
'*Orthoceras*' *gregarium* (J. de C. Sowerby)*	×	×	3	2	–	–
Phragmoceras sp.	–	–	–	1	–	–
? *Polygrammoceras bullatum* (J. de C. Sowerby)	–	5	–	–	–	–
indeterminate cephalopods	–	28	12	12	11	3
TRILOBITA						
Calymene sp.	–	3	4	25	1	–
Dalmanites myops (König)	25	254	33	73	40	4
Encrinurus n. sp.	–	–	–	35	3	–
Hemiarges sp.	–	–	–	1	–	–
Leonaspis coronata (Salter)	3	21	–	–	–	–
Otarion megalops (M'Coy)	1	–	–	8	1	–
Phacops sp.	–	4	–	–	–	–
Proetus astringens Owens	–	6	6	61	4	–
Proetus obconicus (Lindström)	–	–	–	5	–	–
Raphiophorus parvulus (Forbes)	2	4	–	–	–	–
indeterminate trilobites	–	1	1	3	5	1
PHYLLOCARIDA						
Ceratiocaris sp.	–	1	–	–	–	–
INCERTAE SEDIS						
Conularia sp.	–	–	–	1	–	–
Cornulites serpularius Schlotheim	–	–	2	11	1	2
Hyolithes forbesi (Sharpe)	–	15	8	–	–	–
Tentaculites tenuis (J. de C. Sowerby)	–	–	–	26	2	1
TOTAL INDIVIDUALS	192	5420	1426	8472	4095	833
TOTAL SAMPLES	18	48	21	90	37	11

Table 16 Cumulative faunal content for samples assigned to the following associations: upSw – upper phase of *S. wilsoni*; So – *S. ornatella*; Pl – *P. ludloviensis*. Within each association, samples have been grouped into two taphonomic categories: d – disturbed neighbourhood assemblages; t – transported assemblages. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals

Association	upSw	upSw	So	So	Pl	Pl
Taphonomic category	t	d	t	d	t	d
ANTHOZOA						
solitary trochoid coral	–	2	–	–	–	–
BRYOZOA	47	59	7	32	49	152
BRACHIOPODA						
Atrypa reticularis (Linnaeus)	55	35	21	122	–	8
'*Camarotoechia*' *nucula* (J. de C. Sowerby)	412	579	43	170	367	1091

Table 16 continued

Association Taphonomic category	upSw t	upSw d	So t	So d	Pl t	Pl d
Craniops implicata (J. de C. Sowerby)	1	327	–	–	4	5
Dayia navicula (J. de C. Sowerby)	158	30	1	8	2	26
Dolerorthis sp.	1	–	–	–	–	–
Eospirifer radiatus (J. de C. Sowerby)	–	3	–	–	–	–
Howellella elegans (Muir-Wood)	331	200	24	35	19	34
Hyattidina canalis (J. de C. Sowerby)	353	108	5	6	–	–
Isorthis clivosa Walmsley	–	–	71	78	2	16
Isorthis orbicularis (J. de C. Sowerby)	172	274	–	5	–	–
Leptaena depressa (J. de C. Sowerby) and *Lepidoleptaena* sp.	–	4	13	141	1	1
Leptostrophia filosa (J. de C. Sowerby)	18	1	1	6	–	–
Lingula lewisii J. de C. Sowerby	–	9	1	6	–	15
Orbiculoidea rugata (J. de C. Sowerby)	1	7	1	4	10	24
Protochonetes ludloviensis Muir-Wood	220	173	22	18	1484	1900
Salopina lunata (J. de C. Sowerby)	248	179	102	22	800	366
Shagamella ludloviensis Boucot & Harper*	369	112	5	20	–	–
Shaleria ornatella (Davidson)	42	10	269	130	–	13
Sphaerirhynchia wilsoni (J. Sowerby)	467	192	–	7	–	3
indeterminate spiriferides	–	12	–	–	–	–
GASTROPODA						
Bembexia lloydii (J. de C. Sowerby)	1	4	–	–	–	2
Bucanopsis expansus (J. de C. Sowerby)	1	1	–	1	4	39
Cyclonema corallii (J. de C. Sowerby)	7	10	–	–	5	17
Euomphalus sp.	–	1	–	–	–	–
murchisoniacean sp. A	–	–	–	1	–	–
Oriostoma sp.	–	1	–	–	–	–
platyceratacean sp. A	–	1	–	2	–	3
platyceratacean sp. B	–	–	1	–	–	2
indeterminate bellerophontaceans	1	1	–	–	–	–
indeterminate high-spired gastropods	1	1	–	2	2	9
indeterminate gastropods	11	7	–	–	3	3
BIVALVIA						
Actinopteria sowerbyi (M'Coy)	–	1	–	2	–	–
bivalve sp. D	2	–	–	–	–	–
bivalve sp. E	–	1	–	–	–	1
Cardiola interrupta (J. de C. Sowerby)*	1	1	–	2	–	2
Conocardium sp.	–	1	–	–	1	–
Cypricardinia subplanulata Reed	–	–	–	5	–	–
Cypricardinia sp. A	–	–	–	–	–	1
Dualina striata (J. de C. Sowerby)*	–	–	–	–	–	1
Goniophora cymbaeformis (J. de C. Sowerby)	2	6	–	3	6	39
grammysid sp. B	–	–	–	–	–	1
Grammysioidea sp.	–	–	–	2	–	2
Modiolopsis complanata (J. de C. Sowerby)	–	1	–	–	–	1
modiomorphid sp. A	–	1	–	3	–	6
Mytilarca siluriana Reed	–	–	–	1	–	–
Nuculites antiqua (J. de C. Sowerby)	5	11	6	2	12	89
Orthonota rigida (J. de C. Sowerby)	–	4	–	2	–	–
Palaeopecten danbyi (M'Coy)	1	–	–	1	–	1
'*Paracyclas*' *insueta* Reed	5	16	2	6	3	7
Pteronitella retroflexa (Wahlenberg)	3	9	4	11	2	33

Table 16 continued

Association Taphonomic category	upSw t	upSw d	So t	So d	Pl t	Pl d
Ptychopteria tenuistriata (M'Coy)	5	8	3	10	3	66
Sedgwickia amygdalina (J. de C. Sowerby)	3	33	9	16	18	165
Similodonta sp.	–	–	–	1	–	–
indeterminate bivalves	6	8	3	3	4	12
CEPHALOPODA						
Ascoceras vermiforme Blake	–	–	–	–	–	2
Cyrtocycloceras tracheale (J. de C. Sowerby)	1	–	1	–	2	5
Kionoceras caniculatum (J. de C. Sowerby)	–	–	1	–	–	1
indeterminate cephalopods	3	8	–	1	28	63
TRILOBITA						
Acastella spinosa (Salter)	–	–	–	1	–	1
Calymene neointermedia (R. & E. Richter)	–	–	1	1	–	–
Calymene sp.	1	–	–	–	–	–
Encrinurus stubblefieldi Tripp	–	–	–	2	–	2
Homalonotus knightii (König)	–	–	–	–	–	2
Proetus obconicus (Lindström)	–	1	1	3	–	–
indeterminate trilobites	1	1	1	–	1	2
PHYLLOCARIDA						
Ceratiocaris sp.	–	–	–	–	1	3
EURYPTERIDA						
eurypterid fragment	–	–	–	–	–	1
INCERTAE SEDIS						
Cornulites serpularius Schlotheim	6	2	3	3	8	11
Serpulites longissinus J. de C. Sowerby	–	1	–	–	2	30
Tentaculites tenuis J. de C. Sowerby	15	8	2	4	–	–
TOTAL INDIVIDUALS	2607	2352	619	879	2843	4276
TOTAL SAMPLES	36	38	5	11	29	58

Table 17 An example of the *Glassia obovata* Association in the mudstone facies of the Middle Elton Beds. The samples are from section 1E, Upper Millichope, and provide part of the data upon which Fig. 22 is based. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals. Authorship of specific names can be found in Table 15

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
ANTHOZOA									
solitary trochoid coral	–	–	–	1	–	–	–	–	–
syringoporid	–	–	–	–	1	–	–	–	–
BRACHIOPODA									
*Aegiria grayi**	1	725	5800	1880	1580	86	76	215	26
Amphistrophia funiculata	–	–	–	1	–	–	–	–	–

Table 17 continued

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
Craniops implicata	–	–	3	160	2	3	–	62	2
Dicoelosia biloba	–	–	–	–	–	–	–	–	1
Eospirifer radiatus	–	–	–	–	–	–	–	–	2
Glassia obovata	8	–	5	5	3	–	3	–	4
Howellella elegans	–	–	–	–	–	1	–	–	–
Isorthis clivosa	29	4	2	4	7	25	14	9	21
Leangella segmentum	–	1	–	7	–	–	–	–	–
Lingula n. sp.	–	–	–	–	–	–	1	–	3
Ludfordina pixis	–	–	–	–	–	65	–	–	60
Mesopholidostrophia laevigata	–	–	–	2	2	5	–	–	11
Parastrophinella sp.	12	12	22	4	10	29	3	4	2
Plagiorhyncha sp.	4	12	29	9	36	4	7	13	7
Protochonetes minimus	–	12	12	4	9	4	18	12	10
? *Protozeuga* sp.	1	–	–	–	–	–	2	1	–
Resserella sabrinae nunfieldensis	3	–	2	2	–	–	1	–	–
Skenidioides lewisii	1	6	3	3	1	5	3	–	65
GASTROPODA									
Cymbularia cf. *fastigata*	2	–	–	4	–	–	–	–	–
Euomphalus sp.	–	–	1	4	–	–	–	–	–
gastropod sp. B	–	–	–	1	–	–	–	–	–
Leptozone striatissima	–	–	2	3	–	–	–	–	2
Loxonema sinuosa	1	–	–	–	–	–	–	3	–
pleurotomariacean sp. B	4	–	–	–	–	–	–	–	–
Sinuspira stokei	–	–	–	2	1	–	1	–	–
Temnodiscus salopiensis	–	–	–	–	–	1	–	–	–
BIVALVIA									
bivalve sp. B	–	–	–	–	1	–	–	–	–
*Butovicella migrans**	–	–	2	–	–	–	1	1	–
*Cardiola interrupta**	–	1	–	1	–	1	–	–	1
'*Cyrtodonta*' *perovalis*	–	1	–	–	–	–	–	–	–
*Dualina striata**	1	–	–	–	–	–	–	1	1
Goniophora cymbaeformis	–	–	–	–	–	–	–	–	1
grammysid sp. A	2	1	1	3	–	–	3	4	2
Leptodesma ampliata	–	–	1	–	–	–	–	–	–
modiomorphid sp. D	–	–	1	–	–	–	–	–	1
Mytilarca siluriana	–	–	–	–	–	–	–	2	1
Nuculites pseudodeltoideus	–	–	–	–	–	–	–	–	1
Nuculites woolhopensis	–	–	–	1	3	–	–	–	1
Praectenodonta ludensis	–	1	1	–	–	–	–	–	1
Praenucula sp.	7	2	3	1	–	–	3	2	–
indeterminate pteriaceans	–	–	1	–	–	–	–	1	–
indeterminate bivalves	–	1	–	3	1	1	2	–	–
CEPHALOPODA									
'*Cyrtoceras*' *laevis*	3	1	–	–	–	–	–	3	–
Cyrtocycloceras tenuiannulatum	–	–	–	–	–	–	–	–	1
Cyrtocycloceras tracheale	–	–	1	1	–	–	–	–	1
Dawsonoceras annulatum	1	–	–	–	1	–	–	–	–
Kionoceras caniculatum	–	–	–	–	1	–	–	–	–

Table 17 continued

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
'*Orthoceras*' *dimidiatum**	4	–	6	–	–	–	–	7	6
'*Orthoceras*' *gregarium**	2	5	9	1	7	1	14	8	5
? *Polygrammoceras bullatum*	1	–	–	–	–	–	–	–	–
indeterminate cephalopods*	3	1	–	2	2	3	1	–	1
TRILOBITA									
Calymene sp.	–	–	–	1	–	2	–	–	–
Dalmanites myops	10	4	5	9	5	7	6	8	3
Leonaspis coronata	–	–	–	–	1	1	–	1	–
Raphiophorus parvulus	–	1	1	1	–	–	–	–	–
PHYLLOCARIDA									
Ceratiocaris sp.	–	–	–	–	–	–	1	–	–
INCERTAE SEDIS									
Hyolithes forbesi (Sharpe)	–	–	–	–	1	–	–	1	–
TOTAL INDIVIDUALS	88	59	96	236	86	153	68	126	203

Table 18 An example of the *Mesopholidostrophia laevigata* Association in the calcisiltite facies of the Lower Bringewood Beds. The samples are from section 4B, Ledbury, and provide part of the data upon which Fig. 19 is based. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals. Authorship of specific names can be found in Table 15

Sample number	4B18	4B19	4B20	4B21	4B23	4B24	4B25	4B26	4B27
cm above base of section	4695	4545	4353	4213	3739	3633	3528	3299	2480
Vertical thickness of sample (cm)	40	20	12	15	56	7	10	16	15
ANTHOZOA									
solitary trochoid corals	–	8	–	1	–	–	–	–	2
BRYOZOA	6	11	8	1	5	5	3	3	11
BRACHIOPODA									
Amphistrophia funiculata	5	4	2	1	2	–	2	1	2
Atrypa reticularis	5	3	3	3	57	7	24	20	5
'*Camarotoechia*' *nucula*	3	2	–	4	4	–	–	–	–
Craniops implicata	–	2	1	–	–	1	–	–	–
Cyrtia exporrecta	1	–	–	–	–	–	–	–	–
Dalejina hybrida	1	1	–	1	1	–	–	–	–
Eospirifer radiatus	–	1	–	3	–	–	2	–	–
Gypidula lata	–	–	–	32	2	–	–	2	7
Howellella elegans	14	–	–	–	1	1	–	2	–
Isorthis clivosa	49	13	12	14	40	4	14	9	2

Table 18 continued

Sample number	4B18	4B19	4B20	4B21	4B23	4B24	4B25	4B26	4B27
cm above base of section	4695	4545	4353	4213	3739	3633	3528	3299	2480
Vertical thickness of sample (cm)	40	20	12	15	56	7	10	16	15
Leptaena depressa and *Lepidoleptaena* sp.	8	1	–	3	–	–	–	1	1
Leptostrophia filosa	19	2	–	82	9	–	2	1	1
Lingula lewisii	2	–	3	–	1	–	–	–	–
Mesopholidostrophia laevigata	8	1	1	12	8	2	8	7	2
Orbiculoidea rugata	–	–	–	–	–	1	–	–	–
Protochonetes minimus	–	–	–	4	–	–	1	–	–
'*Schuchertella*' sp.	–	3	1	1	–	–	–	–	–
*Shagamella ludloviensis**	1	2	–	–	2	64	4	–	3
Shaleria ornatella	–	1	–	1	–	–	–	–	–
Sphaerirhynchia wilsoni	47	8	5	4	55	2	6	11	19
Strophonella euglypha	–	4	–	5	–	–	–	1	2
indeterminate spiriferides	–	–	–	–	15	–	3	–	3
GASTROPODA									
Bembexia lloydii	–	–	–	6	2	–	–	1	1
Euomphalus sp.	1	–	1	–	1	–	–	–	–
Leptozone striatissima	–	1	1	1	–	–	–	–	1
Loxonema sinuosa	–	–	1	–	–	–	–	–	–
Oriostoma sp.	–	–	–	–	–	–	–	–	2
indeterminate bellerophontacean	–	1	–	–	–	–	–	–	–
indeterminate gastropods	–	–	–	2	–	–	–	–	–
BIVALVIA									
Actinopteria sowerbyi	–	1	–	–	–	–	1	–	–
bivalve sp. A	–	–	–	–	–	1	–	1	–
bivalve sp. C	–	–	–	–	1	–	–	–	–
bivalve sp. F	–	1	–	–	2	–	–	–	1
Cypricardinia subplanulata	–	–	–	–	1	–	1	–	–
'*Cyrtodonta*' *perovalis*	–	–	1	–	–	–	–	–	–
modiomorphid sp. C	–	–	1	–	–	–	–	–	–
Orthonota rigida	–	–	–	1	–	–	–	–	–
'*Paracyclas*' *insueta*	–	–	–	–	1	–	–	1	–
Ptychopteria tenuistriata	–	–	–	–	–	–	–	1	–
Sedwickia amygdalina	–	1	–	3	–	–	–	–	–
indeterminate bivalves	1	1	4	–	4	–	1	2	–
CEPHALOPODA									
Cyrtocycloceras tenuiannulatum	–	–	1	–	1	–	–	–	–
Kionoceras sp. B	1	–	–	–	–	–	–	–	–
indeterminate cephalopods	–	–	1	–	–	–	–	1	–
TRILOBITA									
Calymene sp.	–	1	–	–	1	–	–	–	1
Dalmanites myops	1	–	1	–	4	–	1	–	1
Encrinurus n. sp.	1	–	1	1	–	1	–	–	–
Proetus astrigens	–	–	–	–	3	–	–	–	2
TOTAL INDIVIDUALS	173	72	49	186	221	25	69	65	66

Table 19 Examples of the upper phase of the *Sphaerirhynchia wilsoni* Association (upSw) and *Shaleria ornatella* Association (So) in the coquinoid siltstone facies of the Lower and Upper Leintwardine Beds. The samples are from section 4A, north of Ledbury, and provide part of the data upon which Fig. 18 is based. Species marked with an asterisk are not included in the final total of individuals; authorship of specific names can be found in Table 16. For taphonomic category of samples: d – disturbed neighbourhood assemblage; t – transported assemblage

Sample number	4A27	4A28	4A29	4A30	4A31	4A32	4A33	4A34	4A35
Association	So	So	So	upSw	upSw	upSw	upSw	upSw	upSw
Stratigraphic unit	ULB	ULB	ULB	LLB	LLB	LLB	LLB	LLB	LLB
cm above base of section	4437	4377	4277	4257	4144	4056	3959	3861	3751
Vertical thickness of sample (cm)	6	9	7	8	8	8	2	2	6
Taphonomic category	d	d+t	d	d	t	t	t	d	d
Bryozoa	–	2	1	–	–	–	1	–	2
Brachiopoda									
Atrypa reticularis	–	12	40	–	–	–	–	–	–
'*Camarotoechia*' *nucula*	10	21	74	17	20	4	9	13	11
Dayia navicula	–	–	–	–	–	–	1	–	–
Howellella elegans	2	14	27	–	3	3	1	–	5
Hyattidina canalis	–	2	6	–	4	3	2	6	6
Isorthis clivosa	1	63	–	–	–	–	–	–	–
Isorthis orbicularis	–	–	–	–	1	3	6	1	1
Leptaena depressa and *Lepidoleptaena* sp.	17	2	52	–	–	–	–	–	–
Lingula lewisii	–	2	1	–	–	–	–	–	–
Protochonetes ludloviensis	7	4	4	3	10	26	6	4	13
Salopina lunata	1	5	12	23	5	3	4	2	5
Shaleria ornatella	–	164	5	–	–	–	–	–	–
Sphaerirhynchia wilsoni	–	–	7	–	2	8	20	20	6
Gastropoda									
Bucanopsis expansus	–	–	–	–	1	–	–	–	–
Cyclonema corallii	–	–	–	2	1	–	–	–	–
indeterminate gastropods	–	–	–	–	–	–	1	–	1
Bivalvia									
Actinopteria sowerbyi	–	–	2	–	–	–	–	–	–
bivalve sp. D	–	–	–	–	2	–	–	–	–
*Cardiola interrupta**	–	–	–	–	–	–	–	1	–
Cypricardinia subplanulata	–	–	2	–	–	–	–	–	–
Goniophora cymbaeformis	1	–	1	–	–	–	–	–	–
modiomorphid sp. A	1	–	1	–	–	–	–	–	–
'*Paracyclas*' *insueta*	1	–	3	–	–	–	1	–	–
Pteronitella retroflexa	4	4	–	–	–	–	–	–	1
Ptychopteria tenuistriata	1	3	2	1	–	–	1	–	–
Sedgwickia amygdalina	1	2	4	13	–	–	1	5	1
Similodonta sp.	–	–	1	–	–	–	–	–	–
Cephalopoda	1	–	–	1	–	–	–	–	–
Trilobita									
Acastella spinosa	1	–	–	–	–	–	–	–	–
Calymene neointermedia	–	1	–	–	–	–	–	–	–
Proetus obconicus	–	–	1	–	–	–	–	–	–

Table 19 continued

Sample number	4A27	4A28	4A29	4A30	4A31	4A32	4A33	4A34	4A35
Association	So	So	So	upSw	upSw	upSw	upSw	upSw	upSw
Stratigraphic unit	ULB	ULB	ULB	LLB	LLB	LLB	LLB	LLB	LLB
cm above base of section	4437	4377	4277	4257	4144	4056	3959	3861	3751
Vertical thickness of sample (cm)	6	9	7	8	8	8	2	2	6
Taphonomic category	d	d+t	d	d	t	t	t	d	d
INCERTAE SEDIS									
Cornulites serpularius	–	1	–	–	1	–	–	–	–
Tentaculites tenuis	–	2	2	–	–	–	–	1	1
TOTAL INDIVIDUALS	49	304	248	60	50	50	54	52	53

Table 20 An example of the *Protochonetes ludloviensis* Association in the coquinoid siltstone facies of the Lower Whitcliffe Beds. The samples are from section 2C, Ludlow, and provide part of the data upon which Fig. 16 is based. All samples are disturbed neighbourhood assemblages. Authorship of specific names can be found in Table 16

Sample number	2C1	2C2	2C3	2C4	2C5	2C6	2C7	2C8	2C9
cm above base of section	2349	2240	2134	1995	1859	1672	1520	1421	1168
Vertical thickness of sample (cm)	7	7	6	7	15	15	12	11	14
BRYOZOA	1	–	1	–	3	1	16	4	2
BRACHIOPODA									
Atrypa reticularis	–	–	–	–	–	–	–	2	–
'*Camarotoechia*' *nucula*	8	7	1	4	21	5	25	28	28
Craniops implicata	–	–	1	–	–	–	1	–	–
Dayia navicula	–	–	–	–	–	3	–	1	1
Isorthis clivosa	–	–	–	–	–	–	–	4	–
Lepidoleptaena sp.	–	–	–	–	–	–	–	1	–
Lingula lewisii	–	–	–	1	–	1	–	–	–
Orbiculoidea rugata	–	–	–	–	1	–	–	–	–
Protochonetes ludloviensis	89	39	44	39	6	22	2	3	10
Salopina lunata	1	3	1	2	5	9	–	1	2
GASTROPODA									
Bembexia lloydii	–	–	–	–	–	–	–	1	–
Bucanopsis expansus	1	–	1	1	2	–	1	–	–
platyceratacean sp. A	–	–	–	–	–	–	2	1	–
platyceratacean sp. B	–	–	–	–	–	–	1	–	–
indet. high-spired gastropods	–	–	–	–	–	–	4	1	–
BIVALVIA									
*Dualina striata**	–	–	–	–	–	1	–	–	–
Goniophora cymbaeformis	–	–	–	–	–	–	–	1	–
Grammysioidea sp.	–	–	–	–	–	–	–	1	–
Nuculites antiqua	–	–	–	–	1	2	–	–	–
Pteronitella retroflexa	–	–	–	1	–	–	–	–	–
Ptychopteria tenuistriata	–	1	–	1	2	1	3	–	–

Table 20 continued

Sample number	2C1	2C2	2C3	2C4	2C5	2C6	2C7	2C8	2C9
cm above base of section	2349	2240	2134	1995	1859	1672	1520	1421	1168
Vertical thickness of sample (cm)	7	7	6	7	15	15	12	11	14
Sedgwickia amygdalina	–	–	1	1	9	6	–	1	3
indeterminate bivalve	–	–	–	–	–	–	–	1	–
CEPHALOPODA									
Ascoceras vermiforme	–	–	–	2	–	–	–	–	–
Cyrtocycloceras tracheale	1	–	–	–	–	–	–	1	–
Kionoceras caniculatum	–	–	–	–	–	–	1	–	–
indeterminate cephalopods	–	1	–	1	4	–	1	1	3
TRILOBITA									
Encrinurus stubblefieldi	–	–	–	–	–	–	1	1	–
indeterminate trilobite	–	–	–	–	–	–	–	–	1
TOTAL INDIVIDUALS	101	51	50	53	54	50	58	54	50

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An asterisk (*) denotes a figure

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